Beetle diversity of chalk river floodplains

Thesis submitted for the degree of Doctor of Philosophy

University College London

by

VICTORIA SHEPHERD

Department of Geography

University College London

December 2013

I, VICTORIA SHEPHERD confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

VICTORIA SHEPHERD

Abstract

Anthropogenic land use changes have increasingly altered and fragmented floodplain landscapes. While the impacts of these alterations are being recognised for many plant and vertebrate taxa, limited information is available for highly diverse invertebrate families. Using a variety of approaches to diversity measurement, this thesis investigates carabid and staphylinid beetle assemblages across a range of chalk floodplain habitats in Norfolk, England. It aims to establish the roles anthropogenic and environmental factors play in shaping their communities in order to inform tailored conservation practices.

Site management was identified as the dominant influence on beetle assemblages, underpinning the development of distinct communities amongst floodplain meadow, fen and woodland habitats. Surrounding landscape configuration also influenced beetle assemblages, confirming the wide-ranging, multi-faceted impacts of anthropogenic land use changes. Beetle communities in floodplain woodlands were both specimen- and species-rich across the highly heterogeneous forest microhabitats hosted within. Functional diversity analysis highlighted the vulnerability of certain functional groups to management and fragmentation. It confirmed the importance of conserving remaining remnants of natural floodplain woodlands to support vulnerable beetle communities. Floodplain fens harboured rare species, while their overall beetle diversity was surprisingly low. This was attributed to their limited habitat extent, fragmented distribution, and potentially legacies of past land use. This thesis suggests that traditional management regimes must be maintained in fen habitats, and their connectivity promoted, to safeguard and restore the unique biological communities supported within.

This study highlights the importance of adopting habitat-specific conservation objectives to ensure the persistence of specialist species, whilst maintaining a matrix of different floodplain habitats to preserve wider catchment diversity. As anthropogenic impacts on floodplain environments will continue, the potential role of beetles in biodiversity research and conservation, and in particular of staphylinid beetles that dominate the floodplain ground fauna, warrants increasing interest and recognition.

Acknowledgements

Over the past five years I have received support and encouragement from a great number of individuals, only some of whom it is possible to give particular mention to here.

First and foremost, I would like to thank my supervisors, Jan Axmacher and Carl Sayer who never failed to support, encourage and have faith in me. To Dr Jan Axmacher who can explain even the most complex of biodiversity statistics, whose attention to detail drove me to finally learn to punctuate academic prose and whose mindfulness about my work/life balance made me slow down, take a step back and really enjoy my PhD. The good advice, support and friendship of my second supervisor, Dr Carl Sayer, has also been invaluable. His enthusiasm for North Norfolk is infectious and his idiom 'there's no such thing as a problem, only solutions' allowed me to keep a level head during fieldwork and will stay with me through every challenge.

I would like to acknowledge the financial and academic support of UCL Department of Geography, particularly in the award of a Postgraduate Teaching Assistantship. I would also like to give thanks to the UCL Graduate School, University of London Central Research Fund and National Trust for contributing financially to my fieldwork.

Thanks also go to the various landowners along the River Glaven and River Bure for site access and generous hospitality, and to Mez de Meyer at the MoD Stanford Training Area. Particular thanks go to all of those in the River Glaven Conservation Group and Dave Brody of the National Trust, whose fantastic work has kept and continues to keep the magic of chalk streams (and their floodplains!) alive. In particular, a special thanks goes to Dr Ian Shepherd whose passion to understand and conserve the River Glaven catchment knows no bounds.

The enduring fieldwork programme would not have been possible without the contribution of many intrepid helpers, so a special thanks goes to Izzy Jones, Tony Leech, Luca Marazzi, Chris Oehlert, Ian Patmore and my Mum and Dad, Veronica and Neil Shepherd. In particular Tony Leech was so generous with his time and on more than one occasion saved me from an inquisitive bull! A special thanks also goes to Ian Patmore for his ingenious inventions to make my life easier and fieldwork more efficient. Additionally, thanks go to Jackie and Roger Rudd at Roper Farm B&B who provided a home from home and taught me a thing or two about cattle farming!

Starting out in coleopterology would have been all the more scary if it were not for the encouragement, knowledge and mentoring of Peter Hammond. I would also like to thank Martin Collier for not laughing at my first attempts at mounting specimens, for verifying many samples and for his contagious passion for beetles.

I am also so grateful to all those who contribute to R, the software which while making my life more frustrating at times, also made statistics accessible, enabled me to access the full potential of my data and also reinvigorated my passion for maths.

Completing this work would have been nigh on impossible were it not for the support and encouragement of my friends and family, thank you for helping me to remain vaguely sane for the last few years in the midst of my PhD, multiple jobs and attempts to maintain a social life. A very important thanks goes to Sue Gibbs whose time and dedication helped me over the final hurdle. Great thanks go to my Mum and Dad (again!) whose car mileage might have seen better days after a fieldwork season, but whose love, support, and unending belief I could not be without. Thanks also to my Grandma, Rosemary Gower-Jones, who provided write-up-facilities-with-a-view and home cooked food to fuel the inspiration. Finally, I am indebted to my husband Rick, who made innumerable sacrifices, countless cooked dinners and provided immeasurable emotional support to enable me to pursue my dream of learning more.

Table of Contents

List of Tables

List of Figures

Rivers and their floodplains have a magic for people that has been captured in art and poetry for centuries, as well as being the most biodiverse and fertile elements recognised in landscape ecology. Their loss is therefore one of the best examples of the economic, social and ecological damage to our community's natural heritage done by commercial exploitation by individuals and organisations, without regard for the well-being of either the present community or future generations. If this were not enough, what of the ethical questions regarding the survival of other species, and our ultimate dependence on them?

(Gardiner, 1998:20)

Chapter 1. Introduction

The loss of biological diversity due to the destruction of natural habitats has been argued to be the most devastating anthropogenic impact, beyond war, economic or energy crises (Wilson, 1984). As in most parts of Europe, humans have transformed landscapes in Britain for centuries (Krebs *et al.*, 1999). It is important to understand the impact of these alterations in order to prevent any further losses in species and impacts on ecosystem functioning. This thesis focuses on the effects of anthropogenic factors on the biological diversity in floodplain environments of Norfolk, eastern England.

1.1 Biodiversity

1.1.1 What is biodiversity?

The term 'biological diversity' has been widely used for many decades before the contraction to 'biodiversity' was coined by W.G. Rosen for the 1986 *National Forum on BioDiversity* (Harper and Hawksworth 1995). For the purpose of this work, the terms 'biodiversity' and 'biological diversity' can be considered synonymous. The following definition was stated in the Convention of Biological Diversity definition of terms (UNEP, 1992):

> *'"Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.'*

The definition above outlines the three distinct levels of biodiversity (Table 1.1): species diversity, genetic diversity within species, and ecosystem diversity. Species diversity refers to the number of species on earth or in a specific ecosystem or taxonomic group, and is the most commonly used measure of biodiversity (Harper & Hawksworth, 1995; Magurran, 2004; Gotelli & Colwell, 2011; Magurran & McGill, 2011b). Genetic diversity refers to numbers of different genes and alleles present

within populations, species and ecosystems (Zeigler, 2007), and ecosystem diversity refers to the number of different ecosystems and their specific communities within a spatially distinct area. Biodiversity can be additionally divided into alpha (α), beta (β) and gamma (γ) diversity (Whittaker, 1960, Table 1.1). α-diversity is the richness of taxa at a specific site or habitat, β-diversity is the difference in the taxonomic compositions between two or more sites or communities, and γ-diversity refers to the species richness within a whole landscape, based on the combination of α- and β-diversity (Whittaker, 1960, 1965, 1972; Sepkoski, 1988; Magurran & McGill, 2011a). However, it has been argued that biodiversity studies should address the question of scale, and rather than focusing on α-, β- and γ-diversity, one should focus on local-, landscape-, and regional- diversity respectively (Whittaker *et al.*, 2001). Furthermore, it is also important to recognise functional processes, such as gene flow, adaptation, connectivity and disturbance regimes, in the definition of biodiversity, as they structure species and communities and are crucial for maintaining biodiversity (Noss, 1990). These aspects are often overlooked and consequently undervalued in biodiversity research (Noss, 1990; Ward *et al.*, 1999). These three hierarchical concepts are combined in Table 1.1.

Table 1.1 The hierarchical nature of biodiversity with selected examples. Adapted from Noss (1990) and Ward et al. (1999).

Level of focus	Composition	Structure	Function
Landscape	γ-diversity	Geomorphic patterns Large-scale environmental gradients Ecotones	Disturbance regimes Connectivity Hydrological processes Atmospheric processes
Community/ ecosystem	α- and β-diversity	Habitat heterogeneity Ecotones	Energy flow Patch dynamics Succession Connectivity
Population/ species	Frequency of occurrence	Microhabitat structure	Life history Meta-population dynamics Adaptation
Genetic	Allelic diversity	Heterozygosity	Gene flow Genetic drift Mutation rate

1.1.2 Measuring biodiversity

There is a vast drive to measure biodiversity in order to understand how it arose, how it is distributed and more recently, how fast it is disappearing (Purvis & Hector, 2000). The measurement of biodiversity began with Charles Darwin's record of plants at a meadow in Downe, Kent, England in 1855, followed 50 years later with the first publication of relative abundance of species by Christen Raunkaier in 1909 (Magurran & McGill, 2011a). However, it was not until the late 20th century with recognition of the global resource of biodiversity and its potential loss that studies measuring and analysing biodiversity increased. These studies greatly enhanced our understanding of the full spectrum of organisms and the origin of such diversity (Ehrlich & Wilson, 1991). However, huge knowledge gaps still persist; even the basic questions regarding the global number of species is far from accomplished (e.g. May, 1988; Stork, 1993; Mora *et al.*, 2011).

In the quest to measure biodiversity, emphasis has largely been placed on measures of species diversity, often expressed using species richness indices and species density estimators which provide an instinctive and natural guide to community structure (Gotelli & Colwell, 2011). These measurements have widely been used to estimate rates of species extinction (e.g. May *et al.*, 1995; Pimm *et al.*, 1995), quantify the influence of anthropogenic activities (e.g. Weibull *et al.*, 2003; Lövei *et al.*, 2006; Liu *et al.*, 2010) and establish goals for conservation (Gotelli & Colwell, 2001; Magurran, 2004).

The ways in which we can divide and measure biodiversity depend substantially on the line of enquiry. However, the quantification of biodiversity is most commonly driven by political and social systems (Purvis & Hector, 2000; The Royal Society, 2003), as governmental and voluntary organisations choose to disseminate and enforce policies based on quantitative criteria, rather than qualitative changes in community structure (Noss, 1990). Yet, the vast scale of all biodiversity combined with the intricacy at which it acts would suggest that its measurement is seldom, if ever, possible. The abstract concept of biodiversity as 'the variety of life' or the 'irreducible complexity of all life' does not allow for a single measure (Gaston, 1996; Williams & Humphries, 1996; Purvis & Hector, 2000). In addition, measuring biodiversity at species level or as a single measurement often assumes that each biota or ecosystem contributes equally within that system, or at least that each ecosystem is given equal weighting (Harper & Hawksworth, 1995; Bengtsson, 1998; Mouchet *et al.*, 2010).

The importance of incorporating differences in species or communities beyond their taxonomic classification has been emphasised for biodiversity research (e.g. McGill *et al.*, 2006; Cadotte, 2011; Gerisch *et al.*, 2012). Measures that attempt to incorporate other elements of species' differences, such as traits or genetic dissimilarities have been established (Gaston, 1996; Mason *et al.*, 2005; Villéger *et al.*, 2008; Mouchet *et al.*, 2010). Trait diversity can be defined at the extent that coexisting species vary in terms of their functional traits, or observable phenotypic characteristics that often influence a species' performance and/or ecosystem processes (Diaz & Cabido, 2001; Poff *et al.*, 2006). This approach to measuring biodiversity allows the synthesis of large and complex datasets into more general and interpretable sets of attributes or traits (Weiher, 2011). Trait diversity is not only used to measure how diverse a community is by how similar or diverse the functional traits of a community are, but is also used as a link between community and ecosystem functioning (Weiher, 2011). Species of the more diverse orders of organisms such as insects vary significantly in terms of morphological traits, which have been used to examine assemblage structure and spatial patterns of biodiversity (e.g. Resh *et al.*, 1994; Ribera *et al.*, 2001; Barbaro & Van Halder, 2009; Lambeets *et al.*, 2009; Barton *et al.*, 2011a). While variations in habitat affinity have been shown to be significantly correlated with these morphological traits (Blake *et al.*, 2003; Barton *et al.*, 2011a), species diversity is not necessarily linked with functional diversity (Diaz & Cabido, 2001; Ewers & Didham, 2006; Clough *et al.*, 2007; Bettacchioli *et al.*, 2012). This suggests that the incorporation of traits into the measurement of biodiversity can provide anther dimension to understanding the 'irreducible complexity of all life'.

An additional facet of biodiversity measurement is the assessment of its monetary value. Measurement of the value of biodiversity has been calculated using not only the direct economic values, such as medicinal and industrial products, but also the ecosystem services that the array of plants, animals and microorganisms supply. These include the maintenance of the gaseous mix of the atmosphere, generating and maintaining soils, pollination and controlling biogeochemical cycles. It has been suggested that without these ecosystem services society could not persist (Ehrlich & Ehrlich, 1992). Attempts to calculate a monetary value for the economic and environmental benefits that these ecosystem functions provide, have produced global figures of $2,928 billion per year, which represented approximately 11% of the total world economy (Pimentel *et al.*, 1997). However, the ecosystem services provided by biodiversity are of such a large scale, that they are said to be invaluable; there is no

substitute or the realistic possibility of man replicating them, thereby implying that biodiversity has an unmatched and infinite value (Ehrlich & Wilson, 1991).

Finally, it must be noted that for the measurement of biodiversity, whether using single or multiple indicators, field and analysis methodologies are specific to species, biota and ecosystems. The measurement and valuation of biodiversity in order to ensure its preservation is a necessary, but at the same time fundamental problem; even if one cannot define specific societal benefits, there is still a value in its preservation which is often overlooked by society (Sober, 1986).

1.1.3 Biodiversity loss

It is broadly estimated that rates of biodiversity loss are currently occurring at 100-10,000 times that of the background rate of the fossil record (May *et al.*, 1995; Pimm *et al.*, 1995; Millennium Ecosystem Assessment, 2005) and this is despite continually increasing conservation efforts (Van Vuuren *et al.*, 2006). In the 1980s, Jared Diamond proposed four main causes of biodiversity loss, forming the 'Evil Quartet': overexploitation, invasive alien species, habitat loss and degradation, and chains of extinction (Diamond, 1984, 1989). Similarly today, changes in biogeochemical cycles, enhancing the mobility of biota, and human-driven land use change are considered the greatest threats to biodiversity (Chapin *et al.*, 2000; Millennium Ecosystem Assessment, 2005, Figure 1.1), and by 2100, land use change is projected to have the largest impact of all (Sala *et al.*, 2000).

Estimates of land transformed or degraded by humanity are between 39 and 50% (Daily, 1995; Vitousek *et al.*, 1997), and the consequences of this land domination, such as species extinctions, are suggested to lag behind these figures (Tilman *et al.*, 1994). Between 10-15% of the Earth's land surface is now occupied by row-crop agriculture or urban and industrial areas and another 6-8% converted to pasture land (Vitousek *et al.*, 1997). Habitat loss, especially at such large scales, has a large and consistently negative effect on biodiversity, yet further and wider effects are triggered by the consequences of fragmented habitats (Fahrig, 2003). Habitat fragmentation can create dispersal barriers to certain species and communities, cause isolation and affect the balance between colonisation and extinction rates (Fahrig, 2003; Kotze & O'Hara, 2003).

The patent influence of human activities on biodiversity, may be the loss of species, but they can also reduce the stability and resistance of ecosystems (Tilman, 1996; Chapin *et al.*, 2000; McCann, 2000) and modify ecosystem processes, both directly through global environmental and ecological changes and through functional shifts in species traits (Tilman *et al.*, 1994; Johnson *et al.*, 1996; Loreau *et al.*, 2001; Díaz *et al.*, 2005; Balvanera *et al.*, 2006, Figure 1.1). Whereas these general consequences are recognised, human needs are continuing to be satisfied at the expensive of altered land use, climate, biogeochemical cycles and species distributions (Millennium Ecosystem Assessment, 2005; Balvanera *et al.*, 2006), and further research is needed to quantify habitat- and taxon-specific responses, to suitably inform biodiversity conservation practices.

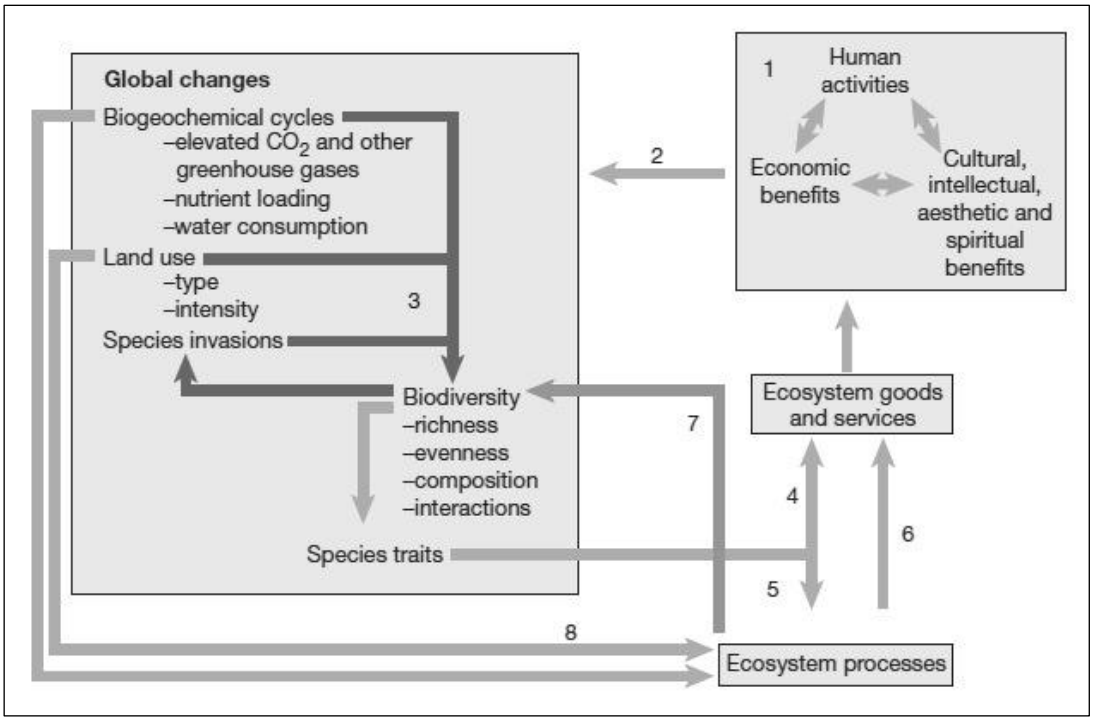


Figure 1.1 Direct and indirect influence of anthropogenic activities on biodiversity from Chapin et al. (2000). Human activities (1), driven by a range of benefits, are causing environmental and ecological changes globally (2). Primarily through biogeochemical cycles, land use and species invasions, these changes are contributing to changing biodiversity (3). Subsequent changes in species and their traits can have direct consequences for ecosystem goods and services (4) and ecosystem processes and functioning (5). Changes to ecosystem processes can in turn affect the goods and services utilised by society (6) and feedback to further alter biodiversity (7). Global environmental and ecological changes may also directly influence ecosystem processes (8), either to a greater or lesser extent than biodiversity changes.

1.2 Beetle diversity

'An inordinate fondness for beetles'. This was the famous response of distinguished biologist J.B.S. Haldane when asked to describe the character of the Creator by studying his creations (a story noted in both Hutchinson, 1959; Farrell, 1998). Haldane's response signifies the known numerical dominance of beetles (order Insecta: Coleoptera) in respect to species numbers, far exceeding any other known plant or animal group (Farrell, 1998). It has been estimated that about one quarter of all species on earth are beetles (Ødegaard, 2000; Hunt *et al.*, 2007; Hamilton *et al.*, 2010). However, to date only approximately 357,000 species have been formally described (Bouchard *et al.*, 2009), and an estimated 70-95% are yet unknown to science (Grove & Stork, 2000). In Britain, there are over 4,000 known beetle species (Cooter & Barcley, 2006).

One of the most important reasons for the success of beetles is the ability of the order as a whole to use a wide variety of food resources in nearly all habitats (Beebe, 1996). Consequently, beetles have adapted to live in every environment. For example Carabidae (ground beetles) alone have populated all habitats except deserts since their emergence in the Tertiary period (Lövei & Sunderland, 1996). Additionally, the development of their elytra, the wing cases or forewings that encase and protect the thin, membranous hind wings used in flight, is suggested to protect beetles against predation and environmental stresses, thus adding to their success (Bouchard *et al.*, 2009).

The two beetle families used in this study are Carabidae and Staphylinidae, the biological classifications of which are given in Table 1.2.

Table 1.2 Classification of Carabidae and Staphylinidae.

	Carabidae	**Staphylinidae**
Kingdom	Animalia	
Phylum	Arthropoda	
Class	Insecta	
Order	Coleoptera	
Suborder	Adephaga	Polyphaga
Superfamily	Caraboidea	Staphylinoidea
Family	Carabidae	Staphylinidae

1.2.1 Carabidae

Carabidae, which are commonly known as ground beetles, are one of the biggest families of Coleoptera, representing 8% of beetle species globally, based on the number of described species (Bouchard *et al.*, 2009). It has been estimated that there are 34,275 species of Carabidae known worldwide (Lorenz, 2005), but new species are continually being discovered. Approximately 2,700 carabid species are currently recorded in Europe, and 350 in Britain and Ireland (Luff, 2007).

Carabid beetles generally have five life stages, namely as larvae, pupae, teneral adult, hibernating adult and active adult, and their habitat preferences often vary according to these different life stages (Lott, 2003). Most carabid beetles have one generation per year, dying after they reproduce (Lövei & Sunderland, 1996); they breed in spring or early summer and overwinter as adults or breed in autumn and overwinter as larvae (Thiele, 1977; Luff, 2006). A few of the larger autumn-breeding *Carabus* spp., *Pterostichus* spp. and *Harpalus* spp. live for more than one breeding season (Lövei & Sunderland, 1996). The larval stage for most spring-breeders is short, but autumn breeding species can spend longer periods as larvae (Luff, 2006). Most larvae live in vertical burrows in the soil, but larvae of *Nebria*, *Notiophilus* and some *Carabus* and *Pterostichus* tribes can be found active on the soil surface (Luff, 2006). Overwintering adult carabid beetles often find habitat in grass tussocks, above water level under bark of old logs, trees stumps, under moss and in flood refuse (Luff, 2006).

In Britain adult carabid beetles range in size from 1.5 mm to 35 mm, but all have a fairly uniform body shape and features. They can be distinguished by their filiform antennae, five segmented tarsi and the hind coxae dividing the first abdominal segment (Luff, 2007, see Appendix 1). Some tribes have adapted morphologies to suit their habitat and eating habits, such as *Clivina* species which have cylindrical bodies and enlarged front legs for burrowing in the soil, flatter species of the *Bembidion* tribe that live in soil crevices and diurnal predators such as species in the *Notiophilus* and *Elaphrus* tribes that have remarkably large compound eyes (Luff, 2006, Figure 1.2). While many carabids use their wings as a primary dispersal method, some species, often larger carabids, have lost their flight abilities. A number of species are also wing-dimorphic with macropterous individuals inhabiting more disturbed habitats and apterous or brachypterous species inhabiting stable habitats.

Adult Carabidae are largely active, terrestrial beetles; 60% of known species are nocturnal and 20% are diurnal (Luff, 1978; Lövei & Sunderland, 1996). Many are

predatory, foraging on the ground surface for small invertebrates. Some species are specialist feeders such as *Cychrus caraboides*, which has protruding mandibles adapted for feeding on snails, and *Loricera pilicornis*, which has long antennae with setae (bristles) used to trap Collembola (Figure 1.2). Other species are general scavengers such as the larger *Pterostichus* species, which will feed on dead prey and on occasion rotting vegetation. A number of species in the Harpalini and Zabrini tribes feed on seeds or seedlings (Luff, 2007).

Carabid assemblages are moderately species rich in temperate environments with 10-40 species often active in a habitat in the same season (Lövei & Sunderland, 1996). When not foraging, carabid beetles often shelter in leaf litter, in the bark of trees, under logs, stones or in soil crevices to reduce predation (Lövei & Sunderland, 1996). Some adult species are widespread, while others are highly restricted to specific habitats. The distribution of carabid species in different habitats can be influenced by several factors including life history, food availability, presence and distribution of predators, and temperature and humidity extremes (Thiele, 1977; Lövei & Sunderland, 1996), the most important habitat characteristic for the majority of species is suggested to be soil moisture (Luff *et al.*, 1989; Sanderson *et al.*, 1995; Antvogel & Bonn, 2001; Luff, 2007).

1.2.2 Staphylinidae

Staphylinidae, commonly known as rove beetles, represent an estimated 13% of all beetles globally (Bouchard *et al.*, 2009), with 55,000 described species worldwide, and over 1,000 recorded in Britain and Ireland (Lott, 2009). They are recognisable by their short elytra leaving their dorsal abdominal section exposed (Appendix 1). While staphylinid species follow a similar life stage pattern as carabids, knowledge of this area is limited and it is possible that rove beetles adopt a wider range of life cycles (Lott, 2003, 2009). Indeed some species of Oxytelinae and Aleocharinae are suggested to have multiple generations each year (Lott, 2003).

Between staphylinid genera, body form is variable with broader species such as *Micropeplus* spp., the more uniform shaped *Quedius* spp. and *Philonthus* spp., to more bullet-shaped species in the Tachyporinae subfamily (Figure 1.3). In Britain, staphylinid beetles range in length from less than 1 mm to 35 mm. This range in body size relates to their differing roles within ecosystems; species with differing body sizes are often segregated in the same ecosystem, as small species mainly live in soil crevices and larger species live at the soil surface (Bohac, 1999). Staphylinid beetles are mainly active during the day, however they show strong preference to dark or shaded habitats

and their maximal activity is influenced by the intensity of lighting (Bohac, 1999). Wings are usually present in staphylinid beetles, folded intricately to fit under their short elytra (Figure 1.3). Most staphylinids can fly but some wings are much reduced in size and some species are apterous (Tottenham, 1954).

Similar to carabid beetles, staphylinid beetles occupy a wide range of habitats (Tottenham, 1954; Lott, 2001, 2009). However, their adult body form is adapted to moving through these environments in a different way. Many adult carabids are said to push their way through soil and leaf litter using physical force, however the longer and flexible bodies of staphylinids' are adapted to weaving through soil crevices, litter and vegetation (Lott, 2009). Around half of the species in the Staphylinidae worldwide are found in ground litter, which makes them one of the most ecologically important insect components of the soil fauna (Bohac, 1999).

The majority of Staphylinidae are thought to be non-specific predators feeding on various soil arthropods, but some are known to feed on fungi, algae, dead plant material and dung (Bohac, 1999; Clough *et al.*, 2007; Lott, 2009). *Quedius* spp. (Figure 1.3) are known to be cannibalistic. Many species have specialised habitats, often representing concentrations of food, such as decaying plant matter or fungi for the subfamilies Micropeplinae, Oxytelinae and Proteininae, or dense populations of prey such as mites, springtails and insect larvae for predatory subfamilies of Paederinae, Pselaphinae, Staphylinidae, and most Aleocharinae (Lott, 2009).

With their specialised life histories, dependencies on other taxa and restrictions in their distribution due to environmental factors (Lott, 2009), staphylinid beetles are considered to be a particularly valuable group for monitoring biological responses to environmental change. In fact it has been argued that, as one of the most encountered invertebrate groups, staphylinid beetles 'should not be ignored in any investigation of biodiversity at whatever scale, site-based, regional or national' (Lott, 2009:1).

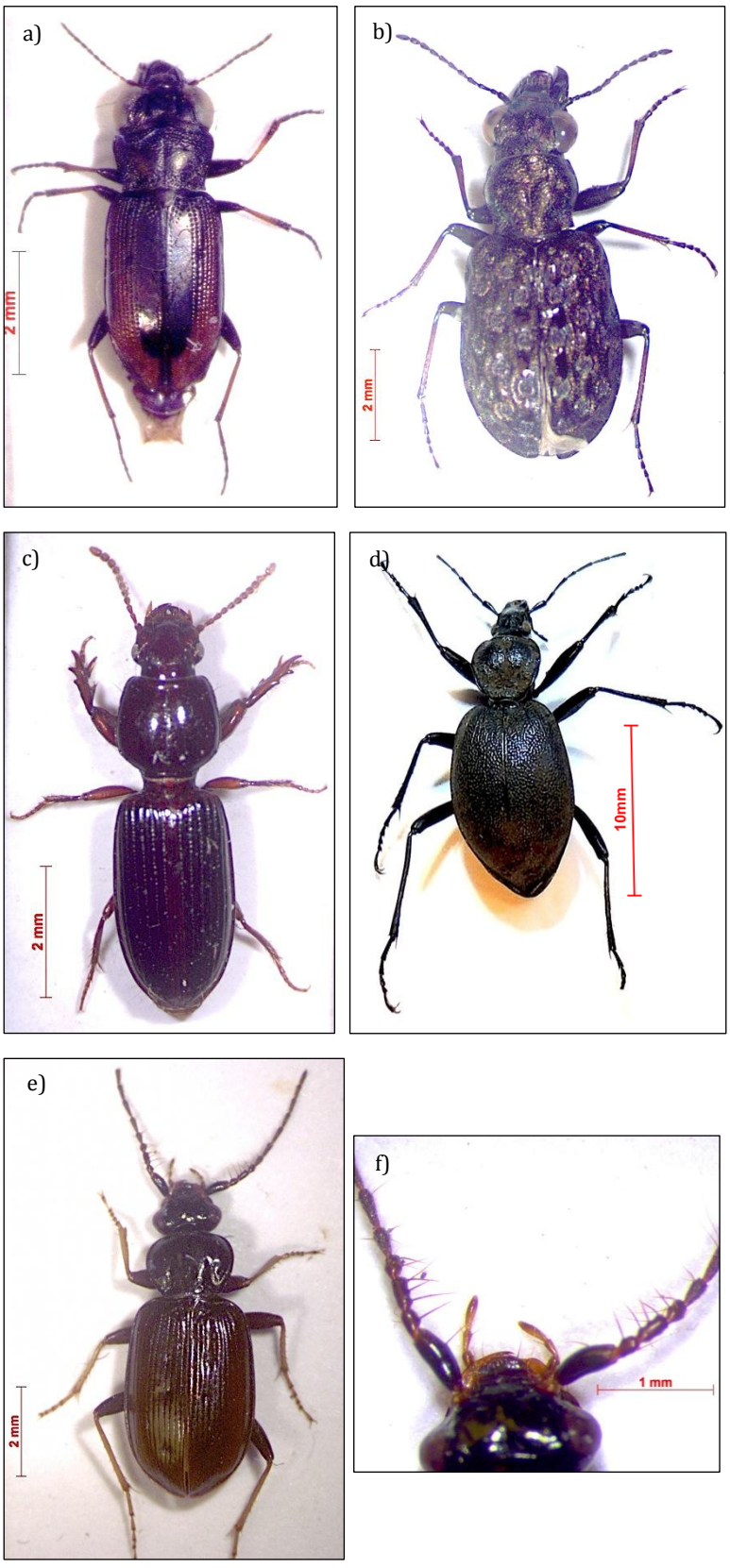


Figure 1.2 Examples of the varying morphology and ecology of carabid species: a) Notiophilus biggatatus *and b)* Elaphrus cupreus *have compound eyes adapted for diurnal predation, c)* Clivina fossor *are cylindrical shaped and have fossorial front legs for burrowing under the soil, d)* Cychrus caraboides *have adapted mouth parts for feeding on snails and e)* Loricera pilicornis *have long setae on their antennae (f) for trapping prey.*

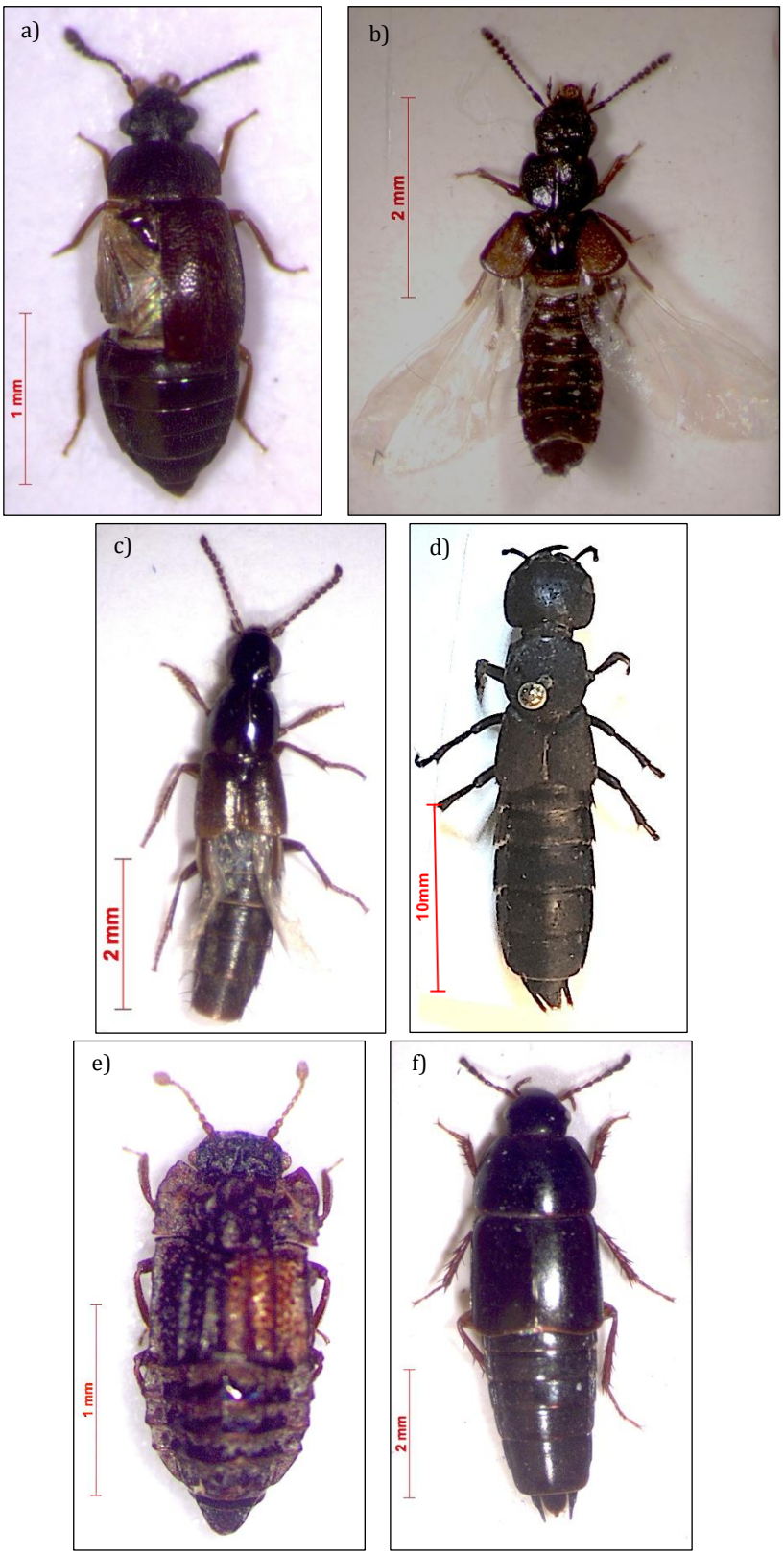


Figure 1.3 Examples of the varying morphology and ecology of staphylinid species: a) Proteinus brachypterous *specimen shows the complex folding patterns that allow wings to fit underneath characteristically short elytra, b)* Platystethus nitens *specimen with its wings fully exposed c)* Quedius schatzmayri*, a more uniformly shaped staphylinid with its wings exposed, d)* Ocypus olens*, one of the largest British staphylinid beetles, d)* Micropeplus staphylinoides *is one of the smallest species of Staphylinidae and feeds on plant material so is often covered with detritus, and e)* Tachinus rufipes, *a distinctive bullet-shaped Tachyporinae.*

1.2.3 Conservation of beetle diversity

Land use changes have not pardoned beetles. In a review of changes in the British beetle fauna, it has been suggested that the impact of humans in the past 5,000 years is likely to have far exceeded that of natural species losses due to historical climate changes (Hammond, 1974). Forest clearance since the Neolithic period has had a profound effect on British beetles, causing considerable retractions in the ranges of forest species and spread of species that prefer open ground (Desender *et al.*, 1994). However, in this respect, at least 300 species of beetles currently found in Britain can be regarded as distinctly favoured by forest clearance, most of which are ground-dwelling forms of Carabidae, Staphylinidae and Silphidae or phytophagous species, associated with weed or ruderal vascular plants (Hammond, 1974). Despite these changes, the conservation of beetles, as with other invertebrates, is often markedly overlooked (New, 2010; Axmacher *et al.*, 2011).

There are great challenges in conserving insects; their specialised habitat requirements, often cause difficulties in the concentration of efforts; in addition to which, different resources are required at different stages of life cycles (Stewart & New, 2007). Furthermore, for some insects the dispersal distances are also comparatively short, so the complex habitat requirements also have to be met within relatively small and fragmented areas (Stewart & New, 2007). Beetles are subject to all of these challenges. As the most diverse group of insects and ubiquitous across ecosystems, they are under considerable threat from anthropogenic changes to natural environments (New, 2010). They are often seen as valuable indicators in conservation research (Pearson & Cassola, 1992; Luff, 1996; Bohac, 1999; Blake *et al.*, 2003; Rainio & Niemelä, 2003; Gerisch *et al.*, 2006; Pearce & Venier, 2006), but nevertheless beetles are commonly not considered as a focus of conservation. Assessment strategies for habitat quality consideration in Britain are largely based on the occurrence of locally scarce or rare plants, botanically defined habitats or the known importance for vertebrate species (see England Field Unit & Nature Conservancy Council, 1990; Rodwell, 1991). Restoration management practices are also largely focussed on plant communities (Bakker & Berendse, 1999; Woodcock *et al.*, 2006; Woodcock *et al.*, 2008). However, site classifications based on vegetation alone may not take account of important structural features in habitats that may be bare of vegetation but provide habitat for numerous invertebrate species (Key, 2000; Eyre *et al.*, 2001a; Eyre *et al.*, 2001b; Blake *et al.*, 2003). Indeed, potentially, beetle-rich, but botanically unexceptional sites may be granted inappropriately low conservation or protection

status based on normal assessment criteria. Consequently, this can lead to inappropriate management of protected areas from the perspective of beetle conservation. Further emphasis should be placed on the conservation of beetles and other invertebrates: 'their staggering abundance and diversity should not lead us to think that they are indestructible. On the contrary, their species are just as subject to extinction due to human interference as are those of birds and mammals' (Wilson, 1987: 345).

1.3 Floodplains

1.3.1 Definitions

Floodplains can be defined as areas of low lying land subject to inundation by lateral water flow from associated rivers or lakes (Junk & Welcomme, 1990). In this project, the focus is on river floodplains, not those associated with lakes. A similar term, riparian zone, also encompasses the stream channel and can be defined as the interface between terrestrial and aquatic systems (Naiman *et al.*, 1993). These interfaces are often referred to as ecotones, that is narrow transition zones between adjacent patches that possess ecological characteristics between the two differing but relatively homogenous community types (Ward *et al.*, 1999). In floodplain systems these ecotones are formed not only between the river and the adjacent habitat but also between surface water and ground water aquifers (Ward *et al.*, 1999).

1.3.2 Floodplain biodiversity

Floodplains are disturbance dominated ecosystems, subject to regular flood-pulses as a result of natural hydrological and geomorphological conditions (Junk *et al.*, 1989). The exchange of water, sediments, organic matter and nutrients in these flood pulses are considered fundamental in the influencing the structure and functioning of floodplain ecosystems (Junk *et al.*, 1989; Ward & Stanford, 1995; Grevilliot *et al.*, 1998; Clilverd *et al.*, 2013). These regimes continually change local geomorphology, microclimate and habitat formations (Naiman *et al.*, 1993; Naiman & Décamps, 1997) resulting in the most diverse, dynamic, and complex biophysical habitats on the terrestrial portion of the Earth (Naiman *et al.*, 1993; Naiman *et al.*, 2005; Tockner *et al.*, 2008). Disturbance regimes, such as flooding, can be understood as one of the key drivers in structuring ecological communities (Hooper *et al.*, 2005; Díaz *et al.*, 2007) because they not only promote biota adapted to exploit the spatio-temporal heterogeneity (Junk *et al.*, 1989;

Mitsch & Gosselink, 1993; Naiman *et al.*, 1993; Naiman & Décamps, 1997; Ward *et al.*, 1999; Woodcock *et al.*, 2005b), but also provide environmental gradients needed to meet the varying habitat required by fauna during complex life-cycles (Robinson *et al.*, 2002). Consequently, more species of plant and animal occur in floodplain landscape units in temperate ecosystems than any other, by quite some way (Tockner & Stanford, 2002).

For plant species, the frequently disturbed nature of the habitat and shifting mosaic of landforms ensures plant species richness varies considerably in space and time (Naiman *et al.*, 1993; Nilsson & Svedmark, 2002). Plant communities are characterised by specialised and disturbance-adapted species within a matrix of less-specialised and less frequently disturbed assemblages (Naiman & Décamps, 1997). Plants also contribute to the heterogeneity of the environment by regulating light and temperature regimes, providing material as food to both aquatic and terrestrial biota, and as debris influencing stream flow and morphology, regulating the flow of water and nutrients and finally providing a diverse collection of habitats (Naiman & Decamps, 1990; Naiman *et al.*, 1993).

For invertebrates, it is estimated that floodplains in the UK provide habitat for more than half of the approximately 30,000 non-marine species, a huge number in comparison to the less than 2,000 vascular plants and vertebrate species found in the UK (Hammond, 1996). However, the significance of terrestrial invertebrates is often understated; they 'find themselves very much at the 'soft' end of floodplain biodiversity and conservation research' (Hammond, 1998). Staphylinidae and Carabidae are the predominant non-aquatic groups of wetland ground fauna (Hammond, 1998). As suggested in section 1.2.1, soil moisture is the key controlling distribution factor for most Carabidae species, so wetland ground beetle communities differ considerably in species composition in comparison to drier environments, although intermediate species can be found in damp grasslands (Luff *et al.*, 1989; Sanderson *et al.*, 1995; Luff, 2007). Similarly many staphylinid species are adapted specifically for wetland conditions, such as the *Stenus* tribe (Figure 1.4), which walk on the water surface in order to cross the small areas of open water commonly found in floodplains habitats (Betz, 1999; Betz, 2002).

Flooding is proposed to play an important role in structuring riparian beetle assemblages particularly in terms of their physiological traits (Lambeets *et al.*, 2009; Gerisch, 2011; Bettacchioli *et al.*, 2012; Gerisch *et al.*, 2012). Many carabid and

staphylinid species have reproductive cycles adapted to reduce the influence of flooding at more vulnerable stages of life cycles (Lott, 2003), and species with high dispersal abilities are often associated with areas subject to inundation by flood waters (Gerisch, 2011). Research into exposed riverine sediments has confirmed carabid and staphylinid communities specifically adapted to these high disturbance systems (Eyre *et al.*, 2001a; Eyre *et al.*, 2001b; Sadler *et al.*, 2004; Bates *et al.*, 2007). However, it is suggested that many riparian species are adapted to certain degrees of disturbance, and that it is intermediate degrees of flood disturbance that relate to increased beetle diversity (Lambeets *et al.*, 2008). Regardless, the biodiversity contribution within floodplains is not confined to the limits of contemporary flooding but extends beyond this (Hammond, 1998), as species exploit the heterogeneity, high productivity and environmental gradients of these ecosystems.

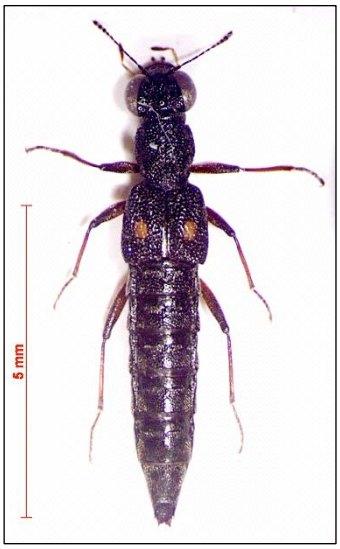


Figure 1.4 Stenus bimaculatus

1.3.3 Anthropogenic impacts on floodplains

'The morphological uniqueness of each river and its floodplain have been achieved throughout millennia without the influence of human activities' (Gardiner, 1998). This has changed dramatically in recent centuries (Zedler & Kercher, 2005), as the 'taming' of river systems has been seen as a primary goal in river management (Heuvelmans, 1974; Brookes, 1988; Purseglove, 1988; Pinter, 2005). Of the estimated two million hectares of floodplain existing in England and Wales around 2,000 years ago, less than 274,000 remained at the end of the 20th Century, as a result of wetland drainage, river engineering, and conversion of former floodplain environments principally for agriculture (Newbold *et al.*, 1989). In Europe and North America, it is estimated that up

to 90% of floodplains have been cultivated thus rendering them functionally extinct (Tockner & Stanford, 2002).

Early forest clearings

The natural vegetation of most British floodplains consisted of a complex and changing mosaic of different woodland types, occasionally interspersed with grassland areas (Hughes *et al.*, 2001). This would not be apparent looking at British riverine landscapes today; in urban areas, developments cover floodplains and in agricultural areas, simply structured grasslands often inhabit the raised banks that disconnect floodplains from their parent rivers.

Although it is indisputable that the majority of this anthropogenic impact results from changes within the last couple of centuries, the burgeoning research of alluvial archaeology is providing solid evidence for early civilisations' use of river floodplains in prehistoric times (Howard *et al.*, 2003). Considerable declines in floodplain forests resulting from human deforestation have been revealed from pollen evidence at a number of sites in England (Smith, 1970; Brown, 1988, 1997), suggesting that most floodplain forest clearance in Britain occurred in prehistoric and early historic times (Peterken & Hughes, 1995).

Floodplains agriculture and river regulation

Floodplains are currently synonymously associated with intensive agriculture owing to their highly fertile soils and the historical role of rivers as communication routes for trading (Bailey, 1998; Tockner & Stanford, 2002; Verhoeven & Setter, 2010). By 1985, it is estimated that 56-65% of available wetland had been drained for extensive agriculture in Europe and North America (Millennium Ecosystem Assessment, 2005).

Despite early vegetation change and drainage of floodplains, it is proposed that the majority of damage to UK floodplain ecosystems was carried out in the 'dig for victory' campaign of World War II, where farmers were encouraged to drain wetlands to increase agricultural outputs (Gardiner, 1998; Acreman *et al.*, 2007). Expanding agricultural practices onto floodplain areas like this required further intensification in management activities including more severe drainage schemes, more frequent use of fertilizers, and the development of exhaustive pastures (Grevilliot *et al.*, 1998). Remaining areas of structurally complex natural riparian forest were commonly replaced by simply structured grasslands as traditional floodplains became utilised for pasture (Harrison & Harris, 2002). Although small fragments of woodland are still

scattered across lowland floodplains, these are invariably secondary in nature (Peterken & Hughes, 1995).

In addition to direct conversion of floodplains, river management and land drainage engineering also altered floodplain environments. These practices were well advanced by 1700, but records of embankments for flood control and land reclamation date back to the 11th century (Petts, 1990b). River channelisation increased even more dramatically in the 19th century, as large sections of river banks absent of trees caused increased flooding in many European rivers and the consequences of the clearance of alluvial forest became evident (Petts, 1990b). In addition to agricultural developments on floodplains, settlements have been consistently located in the vicinity of floodplains, often leading to flood defence methods to protect urban environments. In the UK, channelisation is favoured as a flood prevention method owing to considerable socio-political pressure following flood events (Gardiner, 1998).

1.3.4 Consequences of anthropogenic impacts for floodplain biodiversity

Although it has been suggested that the 'reclamation' of floodplains by humans has been fundamental in the advancement of civilisation (Petts, 1998), the scale of loss of lowland flora and fauna communities resulting from such actions 'can scarcely be overstated' (Hammond, 1998: 239). Inland water ecosystems over the world are suggested to be in worse condition overall than any other ecosystem type (Millennium Ecosystem Assessment, 2005). The importance of riverine landscapes for biodiversity is unquestionable and the consequences of land use change and human domination of ecosystems have been highlighted in Section 1.1.3. More specific impacts to floodplain biodiversity are outlined below.

Consequences of floodplain forest removal

It is suggested that the extent and diversity of natural floodplain forests and the early fauna associated with them would have been larger than communities found in remnant and fragmented areas of semi-natural floodplain forest in Britain today (Drake & Sheppard, 1998). Bronze Age and other 'subfossil' discoveries at UK floodplain sites in particular, have provided more specific indications of the special assemblages of terrestrial arthropods. Evidence of lost invertebrate species from floodplain woodlands have been unveiled, including 29 species of beetles known only as subfossils (Buckland & Dinnin, 1993).

Further research on remnant floodplain forests in Central Europe has also suggested important fauna associated with these habitats that may be lost in British landscapes. Alluvial *Quercus–Ulmus* forests have been found to provide habitat for some rare and endangered carabid and spider species, whereas strongly regulated rivers in comparison can be impoverished of stenotopic hygrophilous species (Bonn *et al.*, 2002). In addition, one would expect a considerable decrease in saproxylic communities of insects, in particular beetles, with the reduction of floodplain forest as natural disturbance regimes in these environments cause higher densities of fallen trees (Trémolières *et al.*, 1998).

The destruction of floodplain forests and the creation and management of more open habitats is not simply a story of species depauperation. In fact, it has led to an increase in certain species and in certain habitats which are now protected under conservation legislation such as Biodiversity Action Plans (Maddock, 2008). For example, the creation of fen habitats on floodplains through draining and continual management using cutting, grazing or burning techniques, has led to diverse plant and animal communities. Other open floodplain environments created through the removal of floodplain woodland include certain types of floodplain meadows that provide rich habitats for a diverse range of wildlife. Approximately 500 vascular plant species have been recorded from wet meadows and associated drainage channels (Thomas *et al.*, 1995), and over a thousand notable invertebrate species (Drake, 1998). Some bird, fish, amphibian, reptile and mammal species are also strongly associated with floodplain meadow habitats.

Although some floodplains are proposed to hold diverse terrestrial arthropod assemblages as a result of human intervention, these communities only 'may' include floodplain specialist species (Hammond, 1998). Questions have been raised over anthropogenically modified floodplain communities: 'these may be interesting scientifically but unless they provide conditions which favour the survival of species which are otherwise rare or under threat they contribute little to conservation' (Hellawell, 1988: 443). In these latterly discussed cases they do provide habitat of conservation interest, however one must not forget the *natural* habitats of floodplain environments and their associated biota.

While the clearance of floodplain forests has created different habitats, it has also led to a highly fragmented landscape; a mosaic of different floodplain land use types differing in management. Quantification of the influence of this fragmentation on biodiversity in

floodplain environments is limited, yet evidence from agricultural and other landscapes suggests that the reduction in the sizes of habitats combined with increasing isolation has caused considerable impacts to biodiversity (Gutzwiller, 2002; Fahrig, 2003; Hendrickx *et al.*, 2007). Communities in fragmented environments are structured by their ability to act upon landscape disturbance (Lambeets *et al.*, 2008; Bettacchioli *et al.*, 2012), thus species that can disperse between habitat patches are often favoured, as are generalists that can supplement their resource requirements by utilising more than one habitat type (Dunning *et al.*, 1992).

Consequences of floodplain drainage and channelisation

Flood prevention methods such as disconnecting floodplains from their parent rivers can have considerable consequences for floodplain biodiversity. Channelisation can alter disturbance regimes that are essential for natural plant succession in floodplain environments (Hughes & Rood, 2001). Reductions in water supply often forces a decline in hygrophilous plant species dependent on shallow water tables or perennial stream flow, meanwhile species characteristic of drier areas of the floodplain may be unaffected or expand into areas once occupied by wetland species (Stromberg, 2001). While the influence of channelisation on terrestrial invertebrates has seldom been evaluated, many species are highly sensitive to moisture levels. For example, species compositions of carabid beetle communities on embanked floodplains sites have shown distinct decreases of stenotopic hygrophilous species (Bonn *et al.*, 2002).

1.3.5 Floodplain conservation and restoration

The continuous and widespread modification of natural river environments and the realisation of its consequences, have brought about new era of river and floodplain management, conservation and restoration (Osborne *et al.*, 1993). In riverine environments, restoration practices have involved the reintroduction of a diverse range of structures to increase river heterogeneity, the reconnection of rivers with their respective floodplains and the regeneration of semi-natural floodplain environments. Traditional approaches to riverine conservation and restoration in the UK have been ecologically driven, with species conservation and habitat improvement as the main objectives. However, more recently geomorphological processes have been incorporated into river restoration projects in attempts to recreate more self-sustaining and natural systems (Clarke *et al.*, 2003).

The restoration of semi-natural floodplain grasslands (or alluvial meadows) has become relatively common (e.g. Straškrabová *et al.*, 1998; Bischoff, 2002; Donath *et al.*, 2003; Bissels *et al.*, 2004), which often involves the incorporation of grazing practices (McDonald, 2001; Woodcock *et al.*, 2006). Conservation ethos has commonly been to conserve open landscapes such as these and so floodplain forests have been neglected. However, this is largely but understandably because few fragments of such environment remain in Britain and restoration prospects have been poor (Peterken & Hughes, 1998). Not only this, but limited information is available on the biodiversity of these forest ecosystems to serve as targets for restoration.

While restoration in particular is a important trajectory for these heavily impacted floodplain environments, targets for restoration are arbitrary with decisions made upon specific past time periods or states as the target for restoration (Davis, 2000); this not only implies a static character of ecosystems but is an impossible goal due to the changes in climate, absence of certain species and the introduction of others. As there is little information about the biodiversity of floodplain forests in Britain, a problem can be recognised in defining targets for the restoration of these ecosystems (Peterken & Hughes, 1995). Furthermore, restoration projects often fail to incorporate anthropogenic activity, which will inevitably influence the long-term success of restoration efforts (Brookes & Shields, 1996). Questions can also be raised over whether floodplain restoration can simply be achieved by re-establishing traditional management practices or whether *natural* states should be targeted (McDonald, 2001; Woodcock *et al.*, 2008), and one mustn't disregard or forget the option of natural recovery as a pragmatic method for river restoration (Brookes and Shields, 1996b).

Finally, the evaluation of the effectiveness of river restoration projects is often limited or inadequate (Bernhardt *et al.*, 2005; Roni, 2005; Bernhardt *et al.*, 2007), and when monitoring is implemented, these efforts are usually directed and limited to the responses of floral communities to restoration, with invertebrates rarely considered (Woodcock, 2005). Restoration practices based solely on vegetation are incomplete, as the comparatively low diversity and slow response of plant communities to changes can result in misinterpretation of trajectories, and additionally some habitats may be bare of vegetation but nonetheless provide habitats for numerous animal species (Benstead *et al.*, 1997; Key, 2000; Blake *et al.*, 2003).

1.4 Context for this thesis

In Britain, floodplains have been considerably impacted by human activity from prehistoric times, leaving only remnant fragments of natural or even semi-natural floodplain habitats. Despite difficulties in measuring biodiversity, there is a need to assess the status and current value of floodplain ecosystems in order to inform conservation policies. While increasing attention has been paid to the ecology and biodiversity within rivers, the importance of floodplain habitats for local and catchment biodiversity has largely been understated. In particular, floodplain forests have received little research attention with regards to the biodiversity they harbour. Furthermore, conservation policies and research that underpins them are commonly based on plant and vertebrate taxa while, highly diverse orders of insects, such as beetles, have been overlooked. As the predominant non-aquatic groups of wetland ground fauna, further research is needed to understand the responses of beetle assemblages to anthropogenic influences in floodplain environments with the aim of informing conservation and restoration practices.

1.5 Aims and research questions

In view of the aforementioned knowledge gaps in beetle biodiversity and floodplain research, this thesis aims to examine the response of carabid and staphylinid beetle assemblages to the spectrum of management practices and resulting habitat types that typify lowland British chalk floodplains, with a particular focus on floodplain woodlands. Chalk rivers and their floodplains have been heavily influenced by anthropogenic activity, and as England hosts the highest concentration of chalk rivers in Europe, there is increasing recognition of the need to understand and conserve these sensitive ecosystems. The following research questions will be addressed (in the chapters indicated in brackets):

- Do specific management practices on chalk rivers floodplains support distinct beetle assemblages? (Chapters 3 & 4)
- How are these communities influenced by anthropogenic factors at multiple spatial scales? (Chapters 3 & 4)
- How are carabid and staphylinid beetles distributed within floodplain forests? Are there any specific microhabitats of particular importance for the protection and enhancement of beetle diversity in these habitats? (Chapter 5)

- Do functional approaches to the measurement of beetle diversity provide additional perspectives for conservation and restoration practices in floodplain environments? (Chapter 6)

1.6 Thesis structure and outline

This thesis will be presented in a format where distinct chapters concentrate on individual research questions, all contributing to the overarching aim of the study (Figure 1.5). The general introduction given in this chapter has outlined the topics that will be addressed in this thesis. A more detailed overview of British chalk rivers and their floodplain habitats, as well as introductions to the study area and study sites will be provided in Chapter 2. Chapters 3-6 are data chapters that contain the bulk of the analysis, each of which will provide a specific introduction, an overview of the analytical methods used and separate results, discussion and conclusion sections. The final concluding Chapter 7 will summarise the findings, discuss overall implications for floodplain conservation whilst highlighting the need for future research. The structure of data Chapters 3-6 are given below.

Chapters 3 and 4

These chapters will address the α- and β-diversity, respectively of beetle assemblages on 15 chalk river floodplains, and assess the influence of a range of site and landscape scale anthropogenic factors on these communities. A series of α-diversity measurements will be used in Chapter 3, not only to most suitably summarise and compare beetle α-diversity in and between these habitats, but also to address the importance of analysis methodologies in the realm of biodiversity conservation. Multiple linear regression will be utilised to identify significant anthropogenic influences on the α-diversity of these communities and furthermore, indicator species analysis will be performed to identify characteristic species of management practices and habitat types. In Chapter 4, multivariate variance analysis methods will be used to quantify within- and between-habitat compositional heterogeneity, while redundancy analysis (RDA) and partial RDA will be used to identify the relative contributions of local and landscape factors on beetle community composition. Lastly, Mantel tests will be calculated to examine similarities in cross-taxon communities.

Chapter 5

This chapter will address beetle biodiversity at a different scale by exploring how beetle assemblages are differentiated across microhabitats within a single floodplain forest. To assess how microhabitats and component species are distributed and to identify specific abiotic and biotic factors of importance, analysis of variance (ANOVA), regressions analysis, RDA, pRDA and indicator species analysis will be conducted. Furthermore, Mantel tests will be used to assess the influence of spatial distribution and vegetation composition on beetle communities at this microhabitat scale.

Chapter 6

Finally, a functional trait approach will be used at both macrohabitat and microhabitat scales to further understand beetle community composition and responses to anthropogenic and environmental gradients. To examine the functional diversity of communities as a whole, a selection of functional diversity indices will be performed. ANOVA, RDA and pRDA will be used to identify specific functional traits important in these floodplain environments and additionally to understand the dominant microhabitat, site and landscape factors influencing the functional traits of beetle assemblages. To further address similarities in carabid and staphylinid beetle communities and to establish any parallels in the taxonomical and trait-based classifications of beetle assemblage, Procrustes analysis will be performed.

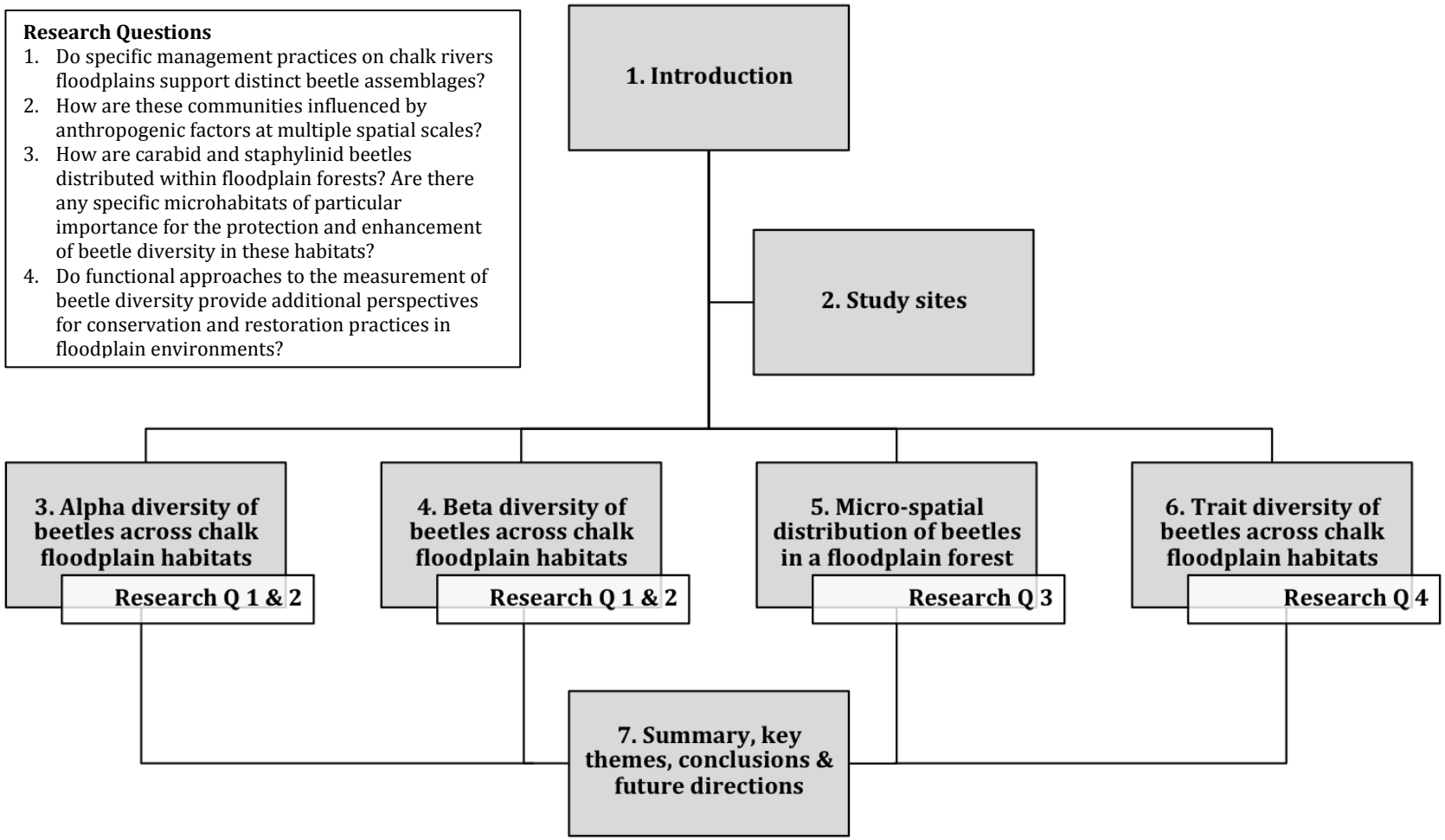


Figure 1.5 Thesis structure in relation to research questions

1.7 Glossary of terms

A list of terms commonly used in this thesis to address the multidimensional aspects of biodiversity in floodplain habitats.

Table 1.3 Glossary of terms

Terms	Definition
Alpha (α) diversity	The richness of taxa within a site or habitat.
Anthropogenic	Originating from human activity.
Apterous	A species lacking wings.
Assemblage	The individuals of all species that potentially interact within a single patch or local area of habitat. Used interchangeably with 'community' within the context of this research.
Beta (β) diversity	The difference in the composition between two or more sites or communities.
Brachypterous	A species with reduced or undeveloped wings, and therefore the inability to fly.
Community	The individuals of all species that potentially interact within a single patch or local area of habitat. Used interchangeably with 'assemblage' within the context of this research.
Ecotone	Narrow transition zone between adjacent habitat patches that possesses ecological characteristics between the two differing but relatively homogenous community types (Ward *et al.*, 1999).
Evenness	The level of similarity in the proportion of different species in a community.
Fen	Wetlands that receive water and nutrients from surface and/or groundwater in addition to rainfall inputs (McBride *et al.*, 2011) and that are maintained from succession into climax communities through traditional management regimes.
Forest	An area of land covered with trees. Small patches of open canopy may persist within the area. Used interchangeably with 'woodland' within the context of this research.
Gamma (γ) diversity	The diversity within a landscape.
Habitat	An area with the combination of resources and conditions that promotes occupancy by individuals of a given species (or population) and allows those individuals to survive and reproduce (Hall *et al.*, 1997). The term is used within the context of this research to distinguish between areas of different management types, such as meadows, fens and woodlands, which as a consequence of management practices or lack thereof, contain different resources and environmental conditions.

Habitat fragmentation	An alteration of the spatial configuration of habitats within a landscape that involves the reduction in size and isolation of habitat patches.
Hygrophilous species	A species associated with wet or damp habitats.
Landscape	An area composted of a mosaic of interacting habitats viewed at the spatial resolution that corresponds with human perception of surroundings (Forman, 1995; Gutzwiller, 2002).
Macrohabitat	A site or landscape relative to an organisms' size that can sustain a population of the organism over an extended period of time (Lott, 2003).
Macropterous	A species with long wings, which most commonly signifies the ability to fly.
Meadow	An area of grassland subject to management by grazing and cutting regimes. Different meadow habitats have been classified according to specific vegetation communities (Rodwell, 1992), but the term is used more generally, as above, within the context of this research.
Mesophilous species	A species associated with intermediate or moderate habitats in relation to moisture and/or temperature.
Meta-community	A set of discrete communities in the same general geographical area, that may exchange individuals through migration or dispersal (Akçakaya *et al.*, 2007).
Meta-population	A set of spatially separated populations of the same species within the same general geographical area that may exchange individuals through migration or dispersal.
Microhabitat	The minimum part of the ecological habitat that supplies the requirements of a species in its particular physiological state at that time (Luff, 1996, Lott, 2003). For beetles this is considered over scales of less than 10m.
Pasture	An area of grassland subject to management by grazing. Used interchangeably with 'grazed meadows' within the context of this research.
Site	A discrete area of land that can be classified into a single habitat type and is thus subject to the same management practices.
Stenotopic species	A species able to tolerate only a restricted range of habitats or ecological conditions.
Trait diversity	The extent that coexisting species vary in observable morphological and ecological characteristics that often influence a species' performance.
Woodland	An area of land covered with trees. Small patches of open canopy may persist within the area. Used interchangeably with 'forest' within the context of this research.

Chapter 2. Introduction to the study sites

2.1 Chalk rivers

Chalk rivers are watercourses dominated by discharge from groundwater aquifers in the underlying chalk geology. England contains 161 chalk rivers or streams, which is the highest number in Europe (Mainstone, 1999; Environment Agency, 2004, Figure 2.1). Their characteristic stable flow and temperature supports a rich diversity of plants and invertebrate life along with important game fisheries (Maddock, 2008).

About 2 millennia ago, chalk rivers flowed through ill-defined channels greatly shaded by riverbank trees like alder and willow (Smith *et al.*, 2003), but now have been subject to the heavy anthropogenic influences experienced by most rivers in the UK. They have suffered from increasing abstraction, physical modifications for flood defence, drainage and navigation, pollution from industry and fish-farms, land-use changes of floodplains to allow the cultivation of arable crops, and fisheries management including bank modifications, weed cutting and gravel clearance (Smith *et al.*, 2003). Changes to flow regimes have greatly altered the usually stable chalk river environments found in the UK. Many chalk rivers lie in densely populated parts of the south of England where intensive agriculture and urban areas have accelerated run off which can wash out weed beds and spawning gravels (Environment Agency, 2004). Yet in drier weather, extensive abstractions from chalk aquifers have greatly reduced flows and increased siltation. For some winterbournes summer dry periods have been extended for months, causing extensive ecological impacts for freshwater species and associated wetlands (Environment Agency, 2004).

Like other lowland rivers, chalk rivers have also experienced channel modifications such as dredging and channel alterations, however as low energy systems they have less capacity to reassert their channel structure (Environment Agency, 2004). Enrichment from agricultural nutrient and silt run off and sewage treatment works has considerably affected chalk rivers, causing extensive growths of blanket-weed on

previously crystal-clear waters and silt deposits to cover riverbed gravels. This blocks spaces for invertebrates and rooting plants and disrupts spawning habitats for the characteristic brown trout of these rivers (Environment Agency, 2004). Now, chalk rivers are recognised as a priority habitat for protection in the UK Biodiversity Action Plan (Maddock, 2008), and there are on-going plans and actions to improve their habitats, plants and animals along with the restoration of water quality, flows and habitat diversity within these rivers (DEFRA, 1994).

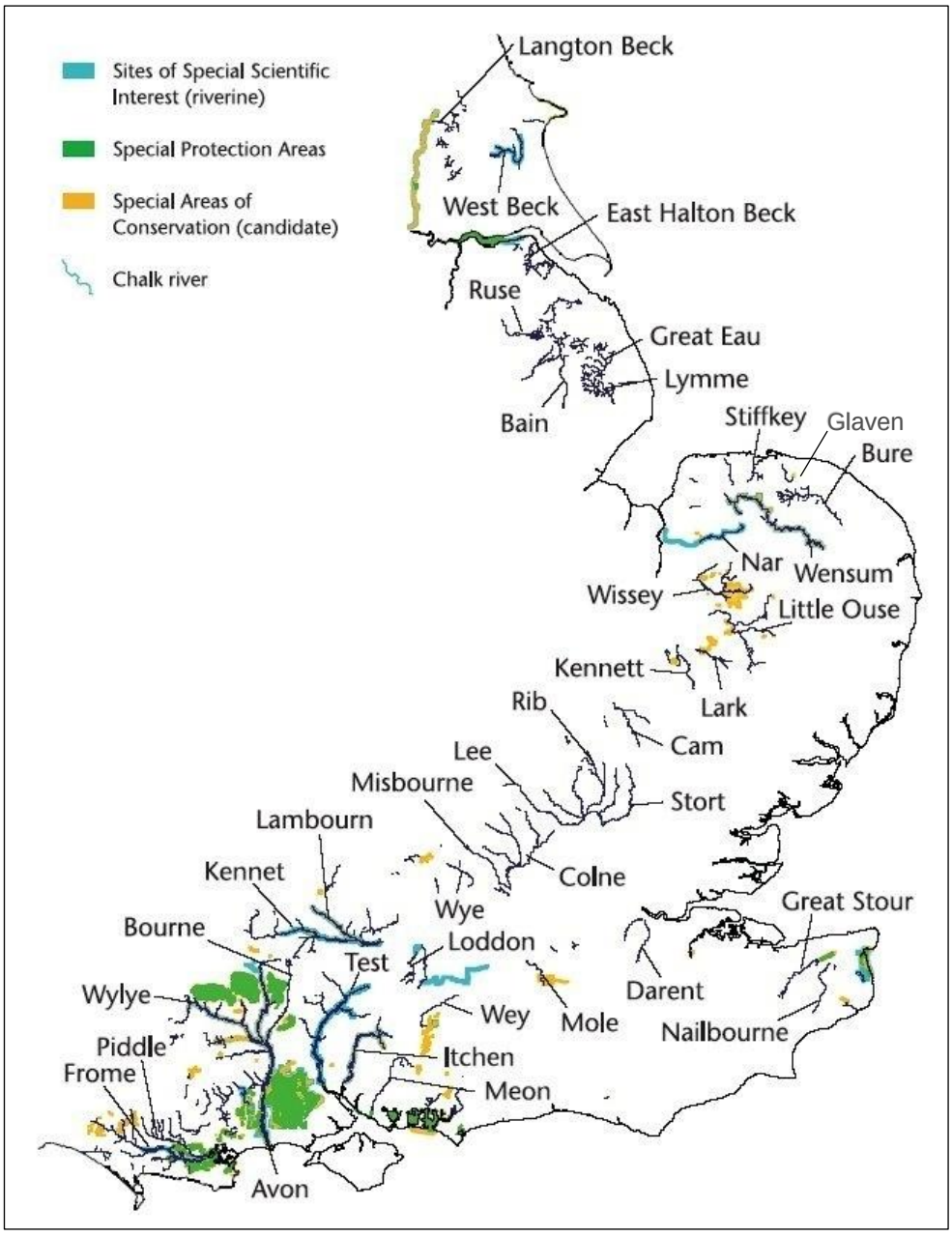


Figure 2.1 English chalk rivers and their associated wildlife conservation designations, from Environment Agency (2004)

2.2 Lowland chalk floodplains in the UK

Attention also needs to be directed at chalk river floodplains, which should be considered in conjunction with in-stream environments, as they are inherently inter-linked. Improved grassland, broadleaf woodland and urban and suburban environments dominate the land use along chalk river floodplains in England, although there are extensive areas of arable land (Environment Agency, 2004). Chalk rivers also support fens, which are dependent upon the groundwater-fed springs and seepages for their water supply (Fojt, 1994). This section will provide an overview of the dominant and fragile environments on chalk river floodplains: floodplain woodlands, floodplain meadows (which vary in grazing and management intensities), and floodplain fens. Urban and arable environments have been excluded from this investigation. While floodplain woodlands and meadows are characteristic of floodplain habitats from all river types, calcareous floodplain fens are a distinctive habitat of chalk river floodplains.

2.2.1 Floodplain woodlands

Semi-natural woodlands can be defined as areas of woodland composed of 'locally native trees and shrubs which derive from natural regeneration or coppicing rather than planting' (Forestry Commission, 2003: 3). Ancient tracts of semi-natural woodlands provide the closest link to original natural woodland in the UK, and include remnants of post-glacial forests, which have never been cleared. As discussed in Section 1.3, woodlands form the natural floodplain vegetation and historically consisted of pedunculate oak *Quercus robur*, ash *Fraxinus excelsior*, elms *Ulmus* spp., willows *Salix* spp., black poplar *Populus nigra*, downy birch *Betula pubescens* and possibly small leaved lime *Tilia cordata* (Peterken & Hughes, 1995). These woodland communities on base-rich soils are often referred to as carr woodland, floodplain woodland or floodplain forest.

Extensive management since prehistoric times has considerably altered these environments and in England; large tracts of ancient floodplain forests have only survived in the New Forest, where strips of 'Ancient and Ornamental' woodland line the Beaulieu River and Highland Water (Peterken & Hughes, 1995). For the majority of floodplains, intensive grazing has prevented any extensive regeneration of woodland vegetation so that most streams 'flow through catchments dominated by arable and pasture land use, with bankside vegetation ranging from grassland to scattered trees

and bushes where cattle have been excluded for many years' (Harrison & Harris, 2002:2234). Nevertheless, small patches of woodland are scattered over lowland floodplains in many parts of Britain; these are secondary and usually occupy particularly wet depressions (Peterken & Hughes, 1995). In some areas such as much of the Broadlands in Norfolk, eastern England, floodplain environments have succeeded to dense alder carr since labour-intensive management was abandoned after the Second World War (Moss, 2001). There are also notable concentrations of secondary wet woodland on fens in East Anglia, Shropshire and Cheshire (Maddock, 2008).

The characteristics of floodplain forests can be deduced from historical sources and remnant near-natural floodplain forests in North America and continental Europe (Petts, 1990a; Peterken & Hughes, 1995). A variety of woodland types co-exist in natural floodplain forests at a range of successional stages, with mosaics of wooded and open habitats; the patterns and compositions of which are determined by the strong land-water interactions and processes (Petts, 1990a; Peterken & Hughes, 1995). Active river channels generate numerous micro-topographical features on these floodplains such as pools, extinct channels and back swamps (Jones *et al.*, 1994):

> *'Great alder trees grew from seedlings on the stools of tussock sedge on the swamp flood and between these stools the peaty pools would swallow you to your waist were you to step in them.'* (Moss, 2001, describing what floodplain woodlands of the Norfolk Broads would have been like in their original state).

The complex and differing environment components are suggested to provide invaluable habitat features for a variety of terrestrial wildlife, dependent on the availability of food resources, flood disturbance regimes, climate and topography (notably at different scales for different taxa) and the order and length of rivers (Peterken & Hughes, 1995). The input of dead wood, detritus from falling leaves, invertebrates from canopies and other organic matter into aquatic habitats also provides food and habitats for stream fauna adapted to take advantage of such inputs (Mason & Macdonald, 1990).

2.2.2 Fens

Fens are wetlands that receive water and nutrients from surface and/or groundwater in addition to rainfall inputs (McBride *et al.*, 2011). There are two recognised categories of fen: 'poor-fens' which are mainly found in uplands on base-poor geology

and 'rich-fens' which are fed by mineral-enriched calcareous waters (Maddock, 2008), such as those along groundwater-fed lowland chalk streams.

As fens are not stabilised 'climax' communities but transitional habitats where pioneer plant communities are replaced by successive colonists (McBride *et al.*, 2011), they require active management through mowing, grazing, burning, peat cutting and scrub clearance, to maintain their open-fen communities and to prevent domination of swards by vigorous plants such as reed canary grass *Phalaris arundinacea* and consequential successional processes into scrub and woodland (McBride *et al.*, 2011). Historically, this management was part of a traditional fen lifestyle; people used fens for grazing, bog-hay production, harvesting reed and sedges for thatching, and peat, reeds and sedge for fuel (Rackham, 1994).

In the UK, as with other parts of Europe, fen vegetation has declined dramatically over the past century (Maddock, 2008). Drainage, conversions to intensive agriculture and abstractions have lowered water tables. Characteristic chalk floodplain communities like fens in East Anglia that are dependent on calcareous spring water, have been considerably impacted by increasing water abstractions from aquifers which not only supply water to these environments but maintain the peat chemistry and so the productivity of fen vegetation (Fojt, 1994). Additionally, the disconnection and consequent isolation of floodplain fens from their associated river has caused considerable changes in the ecology of floodplain fens (English Nature, 2005b). Furthermore, lack or inappropriate management of remaining fens has caused scrub encroachment and succession to woodland environments and agricultural run-off and enrichments have changed natural plant communities (Maddock, 2008).

In intensively farmed lowland areas, little fen area remains and these pockets are small and often isolated. Such pockets can found along chalk rivers where the correct drainage and management promotes their development (Maddock, 2008). Norfolk hosts a large percentage of the UK total fen habitats (Fojt, 1994; English Nature, 2005b), including the calcareous rich fen and swamp of the Broadlands which covers an area of 3,000 ha (Maddock, 2008). However, it is still said that even the larger surviving fragments of fens are degraded in some way, as 'it is rarely possible to preserve a sample and to drain the rest' (Rackham, 1994:195).

Despite its considerably reduced area, the UK holds a large proportion of the fen surviving in Europe. These rare habitats are of high conservation interest and recognised as Biodiversity Action Plan Priority Habitats (Maddock, 2008). They have

the ability to host large and diverse communities of plant and animal species, and certain areas of fen can contain over 250 plant species, some of which cannot be found elsewhere in lowland Britain (English Nature, 2005b).

2.2.3 Floodplain meadows

Floodplain meadows are also not stabilised 'climax' communities and result from the historic and extensive use of floodplains for pasture in the UK. This management results in habitats commonly labelled as 'lowland wet grasslands' (Gowing & Spoor, 1998), and are referred to as floodplain meadow within the context of this research. These meadows consequently require management such as mowing and grazing to remove plant material containing nutrients, preventing the dominance of more competitive species and succession to coarser grasslands and eventually scrub and woodland (Benstead *et al.*, 1997). Although grazing is part of essential management regimes for high-quality floodplain habitats, many riparian meadows have been overgrazed. High stocking densities, causing heavy trampling or poaching, can lead to compaction, increased run-off and sediment loading into rivers, and can accelerate stream bank erosion (McInnis & McIver, 2001). Furthermore, although selective grazing of cattle controls more dominant species such as reed canary-grass *Phalaris arundinacea*, overgrazing of cattle can completely reduce sward height and plant diversity, and consequently insect diversity (Newton, 2004).

Along with overgrazing, there has been considerable loss of semi-natural or high quality floodplain grasslands, caused by agricultural intensification, land drainage, fertiliser use, isolation of floodplains from river flows and abstractions (Benstead *et al.*, 1997). Additionally ecologically insensitive flood defence works have altered hydrological regimes further (Maddock, 2008). It is estimated that of a historical resource of 1,200,000 ha of wet grassland in England and Wales, between 200,000 and 220,000 ha remain (Benstead *et al.*, 1997; Maddock, 2008), with much of the main areas agriculturally improved. Between 1930 and the mid-1980s, an estimated 37% of wet grassland area in the Broadlands was lost (English Nature, 2005a; Maddock, 2008). In Norfolk, estimates suggest that floodplain and coastal wet grasslands cover up to 29,000 ha, which is largely found in the Broads Natural area and North Norfolk Coastal region (English Nature, 2005a).

2.3 North Norfolk chalk rivers

Norfolk's chalk rivers reach a combined length of more than 431 km[a] (Environment Agency, 2004). This study was conducted on floodplain habitats of three chalk rivers in north Norfolk: the River Bure, River Glaven and the River Wissey. These three rivers were chosen for the following reasons:

1. The catchment and riparian land-uses of the study areas are comparable and reflective of floodplains in other chalk river catchments in lowland England. Additionally these catchments had tracts of preserved semi-natural floodplain forests, a declining environment in the UK (Peterken & Hughes, 1995).
2. Areas of the upper River Wissey in particular hold prime examples of semi-natural floodplain forest.
3. Cooperation with riparian landowners enabled access to a range of floodplain habitats. Owners included individuals, the National Trust and the Ministry of Defence (MoD).
4. It was thought that the proximity of the Rivers Bure and Glaven in particular reduced the potential for substantial biogeographical differences in beetle communities.

2.3.1 River Glaven

The River Glaven is 17 km long, has a catchment area of 115km^2 and flows south-westerly from its headwaters in Lower Bodham and Baconsthorpe before turning acutely North at Hunworth and joining the North Sea behind the shingle spit at Blakeney Point (River Glaven Conservation Group, 2013). The river runs through the villages of Hunworth, Little Thornage, Letheringsett and Glandford, before its tidal reaches beyond Cley. The sub-surface geology is predominantly Cretaceous chalk overlain by alluvial sands and gravels of up to 2 m thick (Ander *et al.*, 2006; Clilverd *et al.*, 2013).

Current land-use of the catchment is predominantly arable, intermixed with woodland and a variety of wetland habitats particularly in the tidal regions. Floodplain land-use is predominantly a mix of arable and coniferous plantation in the upper reaches, grazed meadows in the middle reaches and low-lying former washlands in the lower reaches.

[a] Provisional length of Norfolk Rivers calculated using lengths of Norfolk rivers published in Environment Agency (2004)

Similar to most lowland streams, the River Glaven has an extensive history of regulation. Over the centuries, modifications on the river have included channelization through widening, deepening, straightening and embanking, drainage and clearance of floodplains, and the regulation of the river by mills and weirs. Historically, there were 11 water mills on the River Glaven, some of which pre-date the Norman invasion of 1066 (Baker & Lambley, 1983). This suggests a long interrupted water supply for industrial purposes. Five mill structures are remaining today, one is still in operation at Letheringsett. Additionally there are three 'on stream' lakes: Hawksmere (Hempstead mill pond), Edgefield Hall Lake and Bayfield Lake.

Currently, the River Glaven catchment is subject to similar environmental problems of many surface water catchments in England, particularly soil erosion and consequential river siltation, diffuse pollution, over-abstraction and habitat degradation (Southern, 2008). The valley is subject to extensive and intensive arable agriculture, which has resulted in high silt loading in places, including the afforested uppermost sections and arable sections along the Holt Lowes, and Thornage. Abstraction of the River Glaven has been and still is a problem, as surface and groundwater abstraction is considerably 'over-licenced' at low flows (Environment Agency, 2005). These abstractions are primarily used for public water supply, crop irrigation and industrial sand and gravel washing purposes (Environment Agency, 2005; Southern, 2008).

Similar to many chalk rivers, the River Glaven was extensively dredged in the 1970s and 1980s, lowering the river bed and creating high spoil banks to confine the river for flood defence and draining purposes (River Glaven Conservation Group, 2007). The extensive visual impacts of dredging on the River Glaven are suggested in the following quote from a fisherman:

> *'Only yesterday, I walked a stretch of the River Glaven, a tiny stream emptying into the North Sea, for the first time for fifteen or twenty years. Back then, the Glaven was a desert…if you see what I mean. It was pretty well devoid of fish, weed, bank side cover, bends, shallows, pools, anything and everything that makes up the river's natural face. The dredger had just ploughed out everything.'* (Bailey, 2007)

Despite these modifications, there are several stretches of the river that remain in semi-natural form, including sections of semi-natural woodland. Secondary woodlands are situated on the valley floors providing boundaries to the watercourse and are suggested to be natural in content and irregular in form (Watkins *et al.*, 2008). The ecological value of these wet riverine woodlands are suggested to have far more significant a value than those on valley sides (Watkins *et al.*, 2008) and are BAP priority

habitats. The Glaven also holds a number of other important BAP Priority Habitats and has several areas that have been awarded environmental designations (Table 2.1).

2.3.2 River Bure

The River Bure is 80 km long and is one of six rivers that form part of The Broads, the largest protected network of connected rivers and lakes in the UK. The total catchment covers 877 km^2 (Moss, 2001). However the upper catchment, above Horstead, which was the focus of this project covers only 313 km^2 (Hiscock *et al.*, 2001). The Bure flows south-easterly from its headwaters in Melton Constable, with tributaries in Matlaske and Felbrigg, and joins the River Yare at Great Yarmouth before entering the North Sea. The upper reaches flow through the villages of Saxthorpe, Itteringham, Ingworth and Aylsham before the river becomes navigable and part of the Broads at Coltishall. The geological parent material of the catchment, similar to much of the Broadlands area, is formed of glacial till deposits of sands and gravels, over underlying Chalk and Crag (Larwood & Funnell, 1961; Moss, 2001); the river in the upper catchment cuts through both the sands and gravels into the underlying chalk (Watkins *et al.*, 2008). This project focuses on the upper catchment above Aylsham, which is comparable to the River Glaven due to its characteristic chalk river features and size.

Early settlements were located in these upper reaches of the River Bure where areas of forest were cleared to aid hunting in the Mesolithic period (Moss, 2001). Historically, floodplains of the River Bure were not used for intensive agriculture due to susceptibility to flooding. Today the upper River Bure floodplains are a mosaic of land-uses dominated by grazed grasslands interspersed with arable cropping, with willow and alder often lining the river banks (Watkins *et al.*, 2008). Floodplain woodland areas are frequent in the upper reaches and have actually increased on the River Bure floodplains since 1930, however so too has arable farming (Hiscock *et al.*, 2001). The river is still scattered with watermills, including Corpustry, Itteringham, Blickling, Ingworth and Alysham in the upper reaches.

The upper sections of the River Bure provide an important diversity of riverine and adjacent (fen, woodland, wooded carr, wet ditches, grassland and hedges with hedgerow trees) habitats, yet this section of the river has often been ignored in literature. The National Trust holds 140 ha of the river system in these upper reaches and rents it to various farmers and landowners. In a National Trust report, it is suggested that some of the best examples of National Trust wet woodland in the East of England can be found at Blickling alongside the River Bure, in addition to valuable wet

grasslands habitats (Warrington, 2008). These floodplain grazing marshes are marked as 'High' significance UK BAP habitats by the National Trust, with the Wet Woodland of this area to be of 'Medium' significance (see Table 2.1). Effectively the upper region of the River Bure is large enough to support significant populations of Otters and Water Vole as well as transporting species throughout this part of the District. Rather than an extension of the well-recognised Broads region (North Norfolk District Council, 2009), it should be seen as a core area from which to develop connections reaching out into the adjoining terrestrial landscape (see Table 2.1).

2.3.3 River Wissey

The River Wissey is 64 km long (Mason & MacDonald, 2004) and flows from its headwaters in Bradenham, eastern Norfolk, in a westerly and north-westerly direction before joining the Great Ouse just south of Downham Market at the village of Forham. At times of heavy rain, the flow of the River Wissey is diverted along a cut-off Channel just north of Stoke Ferry. The Great Ouse then flows north into The Wash. The upper reaches of the River Wissey flow through the villages of Necton, North and South Pickenham before entering Stanford Training Area (STANTA), a battle training area for the MoD. There it is joined by Watton Brook and streams from two pingo ponds, Thompson Water and Stanford Water. It then flows by Ickburgh, Great Cressingham, Northwold and Stoke Ferry before it joins the Great Ouse. The river course originally flowed further west through the town of Wisbech (Blair, 2006). The geology of the river valley is chalk overlain by Boulder Clay, which is permeable in parts. The river drains the surrounding chalk Breckland and has a naturally regulated flow regime (Petts & Bickerton, 1994).

Relatively little information is available on the history of the River Wissey, and it has been described as 'a river so secret that even its name sounds like a whisper; a river of intoxicating beauty that appears to have somehow avoided the late twentieth century altogether' (Deakin, 1999:197). Historic maps back to 1700s do not suggest considerable changes in the land use, however it is evident visually that the river has been manipulated over the years. Historic parliamentary records from the House of Commons suggest that activities of dredging and widening in order to facilitate further development of agricultural land were carried out in 1943 despite desperate concern for the ecological consequences. Many other occurrences of dredging like this are to be expected of a river this size but records are hard to come by.

Currently, land use in the upper Wissey between Great Cressingam and Northwold, is a mosaic of arable land, pasture and pig farms, and areas of Breckland forests dominated by Scott's Pine, *Pinus sylvestris*. The MoD training ground also hosts a variety of land uses including arable agriculture, pasture, large areas of marshy land and woodland. The River Wissey runs through many tracts of floodplain woodland on its course through the MoD training ground and by Ickburgh village.

Areas of ecological concern on this part of the River Wissey include the considerable pressure of increasing water abstractions for public water supply, industry and agriculture (Petts & Bickerton, 1994). Soil erosion and wash into the river has also been of concern in the upper reaches of the River Wissey in areas of arable fields (DEFRA, 2007). The upper Wissey is also managed as a Trout fishery, which involves the artificial stocking of brown trout.

Table 2.1 BAP Priority Habitats as defined by Maddock (2008), their features and locations on the middle reaches of the River Glaven, and upper reaches of the River Bure and River Wissey, Norfolk. County Wildlife Site - CWS, candidate Special Area of Conservation – cSAC, and Sites of Special Scientific Interest – SSSI.

Habitat	Main conservation features *as defined by Maddock (2008)*	Location, National Grid Reference and Environmental Designations		
		River Glaven	**River Bure**	**River Wissey**
Chalk river	Groundwater aquifer inputs in these habitats produce clear waters, more stable flows and temperatures that support characteristic plant communities, a rich diversity of invertebrate life and important game fisheries, notably for brown trout (*Salmo trutta*). When undisturbed river corridors can develop into rich fen vegetation.	Middle reaches of the River Glaven particularly. The River Glaven is also a notable site for substantial populations of the BAP Priority freshwater species.	The River Bure in its upper reaches is a characteristic chalk river.	The River Wissey is designated as a chalk river and drains large areas of chalk Breckland.
Floodplain grazing marsh	Periodically inundated pasture/meadow and ditches are especially rich in plant and invertebrate species.	Notable meadows include: Thornage Common (TG 060 385) and Hunworth Meadow (TG 068355), which is also designated as a CWS.	Notable meadows include Moorgate Meadow (TG 172304).	Notable meadows include the SSSI designated Hooks Well Meadows (TF 838011) that surround study site Alder Carr.
Fen	Habitats support high diversity of plant and animal communities, particularly plant species, dragonflies and water beetles.	Notable fens include areas of the Holt Lowes (TG 087374), which is designated as CWS, SSSI and cSAC.	No notable areas in this section of the River Bure, however floodplain woodlands hold patches of fen habitat.	The Hooks Well Meadow area has also been assigned as a SSSI based on its base rich fen meadows and acid fen vegetation in hollows (TF 838011). There are also many pockets of marshy fen area within STANTA training areas.
Wet Woodland	High humidity favours bryophyte growth and wet tree species support large number of invertebrate species including BAP Priority beetle, cranefly and moth species. Also provides cover and breeding sites for otter (*Lutra lutra*).	Ares of the Holt Lowes (e.g. TG 092376) and of the Bayfield Estate (TG 046407)	Areas of the National Trust Blickling estate and adjacent land such as Rough Pasture Carr (TG 174303).	Large areas of wet woodland can be found on floodplains within the STANTA training area (TL 838970, TL 832956) and just outside Ickburgh (TL 824950, TL 817947)

2.4 Study sites

Fifteen study sites were chosen from the Rivers Glaven (n=9), Bure (n=5) and Wissey (n=1) (Figure 2.2) to represent the dominant land use types on the floodplain environments of these chalk rivers. A total of five meadows, three fens and seven woodland sites were selected to enable comparison across habitat types and catchments (Table 2.2). The woodland site on the River Wissey represents a natural floodplain woodland habitat, and is part of an area recognised for its rich ground fauna as a result of a long period of stable management (Natural England, 2001).

All sites were less than 50 m above sea level (Table 2.2) and located directly adjacent to their associated river; situated in the middle reaches of the River Glaven, upper reaches of the River Bure and middle reaches of the River Wissey. Factors such as size, drainage and river engineering histories, changes to floodplain land-use and wider catchment changes can have considerable effects on floodplain biodiversity (Hammond, 1998), and consequently have been taken into consideration and recorded in individual site profiles outlined in the following section. Surrounding land use has also been estimated for each study site and recorded as percentages of land use types within a 250 m radius from site perimeter. As hydrological and climate conditions can influence species and communities in these environments, river flow data was obtained for the study rivers (Figure 2.3). However, whilst this information clearly identifies annual and seasonal differences in the hydrological regimes of the rivers, the extent to which this variation conditioned beetle communities cannot be estimated during the two-year fieldwork season. The following section outlines contemporary and historical information for the study sites.

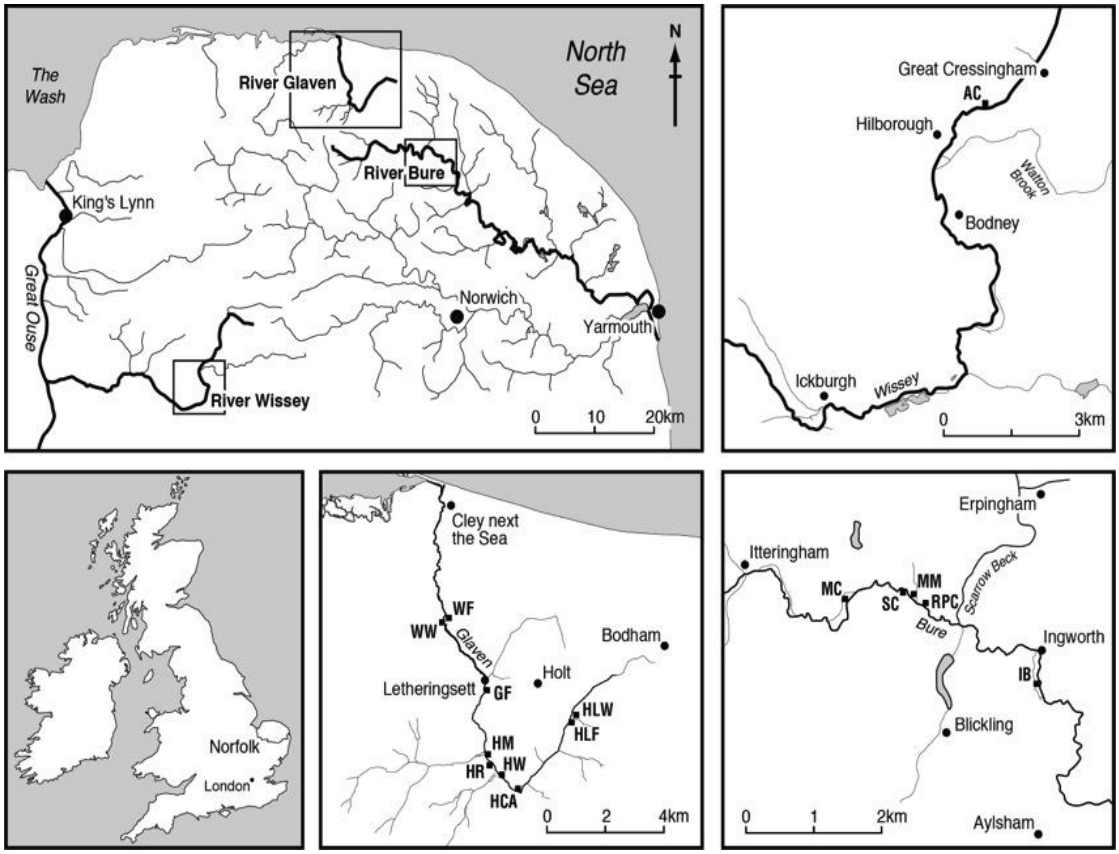


Figure 2.2 Study site locations on the River Glaven, River Bure and River Wissey. Site names are abbreviated (see Table 3.1).

Table 2.2 Floodplain site names, abbreviations, habitat types and catchments.

Habitat	River	Site Name	Site Code	Altitude
Meadow	Glaven	Hunworth Castle	HCA	33 m
Meadow	Glaven	Hunworth Railway	HR	24 m
Meadow	Glaven	Hunworth Meadow	HM	24 m
Meadow	Bure	Moorgate Meadow	MM	18 m
Meadow	Bure	Ingworth Bridge	IB	12 m
Fen	Glaven	Holt Lowes Fen	HLF	48 m
Fen	Glaven	Glaven Farm	GF	15 m
Fen	Glaven	Wildflower Fen	WF	9 m
Woodland	Glaven	Holt Lowes Woodland	HLW	48 m
Woodland	Glaven	Hunworth Woods	HW	29 m
Woodland	Glaven	Wildflower Woods	WW	10 m
Woodland	Bure	Mill Carr	MC	22 m
Woodland	Bure	Shepherd's Carr	SC	19 m
Woodland	Bure	Rough Pasture Carr	RPC	17 m
Woodland	Wissey	Alder Carr	AC	30 m

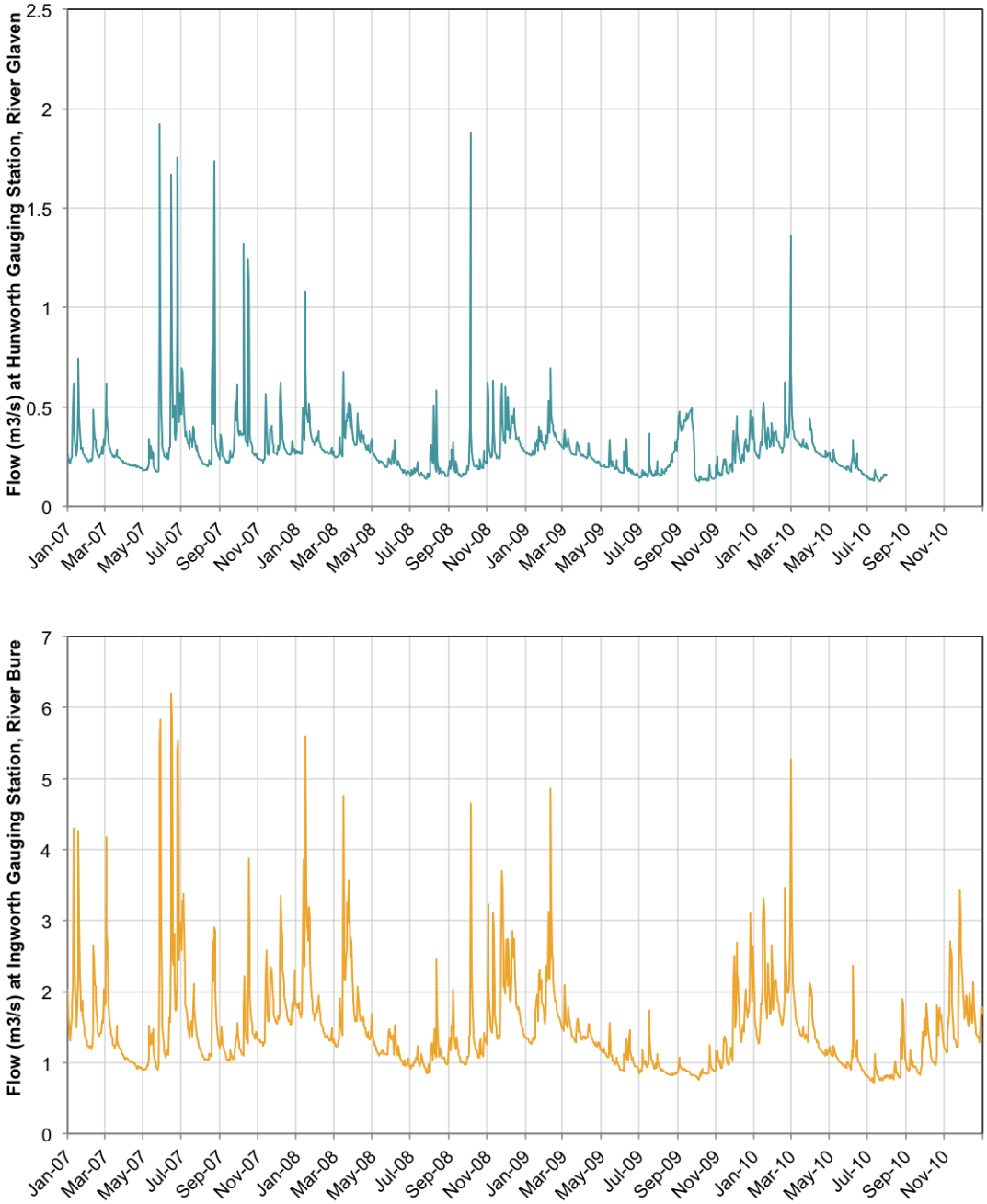


Figure 2.3 Flow rates at gauging stations on the River Glaven and Bure 2007-2010. Data courtesy of the Environment Agency and National River Flow Archive at the Centre for Ecology and Hydrology. No local gauging station data was available to represent hydrological conditions at Alder Carr on the River Wissey. The peak at Hunworth gauging station in March 2009 is likely to be related to the direct influence from the restoration works at that time. Data is not available from August 2010 at Hunworth due to the influence of re-meandering works on the guiding station equipment.

2.4.1 River Glaven

Holt Lowes Woodland - HLW - TG 092376

The Holt Lowes (Figure 2.4-2.5) has been recognised as a SSSI and a cSAC due to its large tracts of heathland and wetlands. HLW was the most upstream study site on the River Glaven, which runs south along the eastern edge of this woodland site. The site consists of carr woodland that has spread onto the open areas of surrounding fen. The site has many underground springs running through to the river. However much of this water seems to be held within the floodplain woodland causing continually high water tables. There are few patches of drier ground, which are found around the bases of trees. HLW is dominated by *Alnus glutinosa* and in some areas *Sorbus aucuparia*, however there is a notable presence of the following other trees: *Betula pendula*, *Corylus avellana*, *Crataegus monogyna*, *Prunus avium*, *Prunus spinosa*, *Quercus robur* and *Salix caprea*.

Although the heathland and wetlands of the Holt Lowes are not natural climax communities; they are old and relatively stable and are suggested to have been in existence for up to 5000 years (Leech, 2000). Since the Bronze Age there is evidence of their maintenance by grazing, burning and periodic cultivation (Leech, 2000). Historically, this wet woodland site, along with the rest of the Holt Lowes, was part of the common land called a 'Poors Allotment', set aside for poorer houses in the parish to use for grazing and small plots of crops. This is evident from Faden's 1797 map of Norfolk. Since the enclosure act of 1807, use of the land steadily declined and by the end of the 19th Century it was used for recreation, with trees covering large areas of the heath and wetland (Leech, 2000). Trees have lined the river in this area for some time but the current woodland at HLW is a result of succession this century into carr woodland. Since the 1960s considerable management attempts have been made to prevent the recolonisation of trees and there is now continual management in place including removal of scrub and woodland cutting, and grazing. There have been 5 cattle that graze the entire area (20 ha) of the Holt Lowes in the summer months since 2008 and rarely enter the wet woodland most likely due to its sinking mud. However, in October 2010 (after sampling) part of the HLW site was felled as part of the on going management activities.

Figure 2.4 Holt Lowes Woodland study site, taken in 2009.

Figure 2.5 Holt Lowes Woodland study site from the River Glaven, taken in 2009.

Hunworth Woods - HW - TG 068355

Hunworth Woods (Figure 2.6) is situated in the middle of Hunworth village, next to a ford crossing the River Glaven, which marks the downstream (north-west) boundary of the study site. The river has two channels at this point, which split just upstream of the site, flow through the site and re-join just before the ford. The main channel has relatively high and steep banks and lies to the south-west of the site, whereas the side channel has shallow banks and strong evidence of undercutting and deposition. The woodland has considerable evidence of previous meanders and courses of the River Glaven including a silted palaeochannel (Figure 2.7). This woodland is dominated by *Acer pseudoplantanus* and in some areas *Corylus avellana* and *Fraxinus excelsior*. *Alnus glutinosa*, *Crataegus monogyna*, *Prunus padus* and *Tilia platyphyllos* were also growing within the woodland. There is a strong dominance of *Allium ursinum* (wild garlic) in the ground flora of the riverbanks surrounding the ford (Figure 2.6)

Historic maps show that this site has been wooded since before the 1880s. There is little evidence of recent management, apart from the felling of two trees presumably as a precautionary measure to protect the close by cottage.

Figure 2.6 Hunworth Woods study site from the south-west bank, looking at the main river channel. The dominance of Allium ursinum *in the ground flora of the banks is evident. Taken in 2009.*

Figure 2.7 Hunworth Woods palaeochannel at the southeastern edge of the site. Taken in 2009.

Wildflower Woods - WW - TG 046407

This woodland site is part of the Bayfield estate (48.5 ha of parkland surrounding an 18th century country house). The site lies to the north of the access road to the country house and is bounded by the main channel of the River Glaven to the east. Upstream of the site, the river divides with one channel bypassing Bayfield Lake to the west, and one channel passing through the lake. The two channels re-join at the downstream edge of WW. The floodplain woodland site is also divided by a number of shallow running waters that run off the diverted (west) channel (Figure 2.8). The main river channel banks are higher than the rest of the floodplain suggesting the river cannot overtop its banks this way, yet the shallow channels that run through the site are able to flood. The woodland has a mixed tree cover, dominated by *Acer pseudoplantanus*, but populated also by *Aesculus hippocastanum*, *Alnus glutinosa*, *Corylus avellana*, *Fraxinus excelsior* and *Sambucus nigra*.

Historic maps show that the site has been wooded since before the 1880s. The site was previously accessible directly from the east side of the river by a walk bridge which has rotted and long since been abandoned. There is some evidence of disturbance along a small strip on the western border of the site, adjacent to the main channel and near the bridge. It is heavily dominated by common nettle, *Urtica diocia* and there is evidence of trees being cut here, most likely for fishing access.

Figure 2.8 Side channel within Wildflower Woods study site, looking south. Taken in 2009.

Hunworth Castle - HCA - TG 074351

This meadow (Figure 2.9) is surrounded on two sides by the River Glaven, the south-east and south-west as the river starts to turn northwards towards the sea. The meadow slopes slightly from north to south with the wettest areas beside the river where vegetation contrasts significantly. It is this lower wet meadow that forms the site. The river is able to flood the meadow, but rarely does so as there is a bridged ford at the upper boundary where the river floods the road at high flows. The meadow is however very damp in the lower sections.

Maps back to the 1880s confirm that it has historically been used for grazing by cattle and sheep. Low levels of inorganic fertiliser were applied in the 1990s until 1997 and since then it has not been improved (Ross Haddow, *pers. comm.*). Most recently it has been grazed during spring and summer months at low intensities and is often used for new born calves and their mothers (Figure 2.10).

Figure 2.9 Hunworth Castle study site looking north-west. The wetter areas to the left comprise the study site. The sloping areas on the right were not sampled. The green flag in the foreground marks the location of a sampling plot. Taken in 2009.

Figure 2.10 Hunworth Castle study site with cattle grazing, looking south. Taken in 2010.

Hunworth Railway - HR - TG 064 359

The River Glaven flows north-westerly through this meadow, accompanied by a slow flowing drainage ditch, which leaves the river two fields upstream and reconnects at the northerly boundary of the site (Figure 2.11). This site is adjacent to another study site Hunworth Meadow, separated by a disused railway bridge. The study site is bounded to the north by this bridge, to the east by a large pasture field, to the south by further floodplain pasture and to the west by the drainage ditch.

Historic maps dating back to 1880s suggest that Hunworth Railway has been open land, and such floodplains have long been used for pasture. The drainage ditch is shown on these historic maps confirming use for agricultural reasons. The site has a similar history to the adjacent Hunworth Meadow and upstream Hunworth Castle meadow and is also owned by the Stody Estate. It has been grazed periodically since 1990 and has been inorganically improved until 1997. In 2009 the site was not stocked but in 2010 it was heavily grazed by cattle from August.

Figure 2.11 Hunworth Railway study site, taken from the disused railway bridge, looking south-east. The river is to the left of the photograph and the drainage ditch is to the right. Taken in 2009.

Hunworth Meadow (HM)

This meadow (Figure 2.12) has been the focus of recent research projects as a result of the river-floodplain restoration practices in 2009 (Clilverd *et al.*, 2013). The meadow is bounded to the north-east by arable and woodland, to the north by pasture, to the west by arable land and a road and to the south, upstream by a disused railway bridge and Hunworth Railway study site. An agricultural drainage ditch runs through the site, on the north-east edge, parallel to the river. It is blocked at the downstream end causing poor drainage at this end of the site.

The river along this reach has been subject to considerable anthropogenic impact largely due to the nearby Thornage Mill. It was straightened around 1800 when a new and larger mill was built (Ian Shepherd, *pers. comm*.). Most recently, restoration work was undertaken in March 2009 to remove approximately 1,400 tonnes of soil from the river embankments in order to reconnect the river and floodplain. Consequently areas close to the river were bare soil when sampling took place in 2009, however no sampling plots were placed in these areas. Additionally the river was re-meandered in August 2010, primarily on the south-west (left) bank to resemble its past form and create backwaters for aquatic species.

Since 1990 the meadow has been grazed by a mixture of sheep and cattle in the spring and summer months. It has generally had low stocking densities but in the year 2000, it was subject to a more intense grazing regime (Ross Haddow *pers. comm.*). Similarly to Hunworth Railway and Castle, low levels of inorganic fertiliser were applied until 1997, but since then it has not been improved (Ross Haddow *pers. comm.*).

Figure 2.12 Hunworth Common study site from the disused railway bridge, looking north-west. The spoil river-bank had recently been removed to reconnect the river with its floodplain. Taken in 2009. Further restoration works were carried out in August 2010 to re-meander this stretch and create backwater habitats.

Holt Lowes Fen - HLF - TG 091375

This fen site (Figure 2.13) is situated adjacent to Holt Lowes Woodland and is part of a larger fen area named Oli's Fen. It is bounded by the woodland to the north, the River Glaven on the east, which is lined with alder trees, more fenland to the south and a rise up to heathland to the west. The ground is extremely wet due to continually high water tables.

The land-use history of this site follows that of Holt Lowes Woodland. It has been managed as a wetland since prehistoric times and there is no evidence of river management along the stretch, such as dredging. Since the 1960s it has been cut biennially. It was most recently cut in June 2008 and in July 2010. Five cattle have been left to graze the entire Holt Lowes area (20 ha) in the summer months since 2008, and regularly grazed at this fen site.

Figure 2.13 Holt Lowes Fen study site, looking north-east. The River Glaven is to the right of the photograph, lined by alder trees. Taken in 2009.

Glaven Farm - GF - TG 061384

This fen (Figure 2.14) is part of a privately owned farm. It is bordered by the tree-lined river to the east, a line of trees to the north, a ditch and further fen meadows to the west and a line of trees and road to the south. Water levels are high in both the fen and within the ditch, which is commonly at full capacity.

Since 1880, maps show this study site to be open agricultural land. It has been suggested that for centuries this land was used for livestock grazing and at one point pig farming, due to the higher financial returns on such a small piece of land (Ian Shepherd, *pers. comm.*) It was still lightly grazed until almost a decade ago but is now managed by the owner using a 'cut and rake' regime in early spring and autumn (Ian Shepherd, *pers. comm.*) For the last 20 years, the river has been ponded back to the ford, just south of the site, to power the restored Letheringsett mill. The mill was originally operated in this way but for the later 1900s it was instead operated through mechanical power (Ian Shepherd, *pers. comm.*).

Figure 2.14 Glaven Farm study site looking east, taken in spring 2009 just after the vegetation had been cut. The ditch is in the foreground and the river is in the distance, lined by trees.

Wildflower Fen - WF - TG 047408

This site is part of the Bayfield estate, and is located close to Wildflower Woods (WW). It is privately rented and has been part of a nature reserve and education centre for several years. It is bounded by the river to the west, meadows to the north, a ditch, further fen areas and wildflower gardens to the east and another fen to the south. The fen is extremely boggy and often contains areas of standing water. Its vegetation is highly diverse and it supports a recognised number of fen-specific plants. Over 1000 orchid heads have been observed within the site in some years (Paul Laurie *pers. comm.*). As a result, the site is enclosed by fencing to prevent access by nature reserve visitors.

Historic maps suggest this area has been continually marshy and open. A ditch that has been used as an eastern border for the site is shown on maps since 1890. Due to the extremely wet conditions grazing is likely to be the only management that has kept it from succeeding into alder and willow woodland. Since Natural Surroundings has been managing the site, it has been grazed approximately biennially. It was last grazed in the winter of 2008-9 by 2 donkeys (Figure 2.15) but not grazed for the rest of 2009 or 2010 (Figure 2.16).

Figure 2.15 Wildflower Fen study site looking west. Taken in April 2009 after winter grazing.

Figure 2.16 Wildflower Fen study site in Oct 2010 after no grazing for 20 months, looking north-west.

2.4.2 River Bure

Mill Carr - MC - TG 162303

Mill Carr study site is a woodland on the north bank of the River Bure (Figure 2.17) and is bordered by pasture to the north and west and by further woodland to the south and east. A drainage channel flows around north of the site to join the river downstream at the eastern edge of the woodland. The varying topography of the site results in very wet areas and drier areas at the base of trees. The canopy is dominated by four tree species: *Alnus glutinosa*, *Fraxinus excelsior*, *Salix caprea* and *Salix triandra*. *Corylus avellana*, *Crataegus monogyna*, *Prunus padus*, *Prunus spinosa*, *Sambucus nigra* and *Sorbus aucuparia* were also present in the woodland.

The site is currently privately owned by a farmer who has left it as woodland protected from cattle intrusion by barbed wire and the old drainage channel. Historic maps suggest that this site and surrounding woodland has been wooded since pre 1880. There is some evidence of coppicing but these stumps have since grown into towering trees so such activities would have been over 70 years ago (Figure 2.18). The river along this stretch has been over-widened and dredged causing heavy silting, and natural wood falling into the river has previously been removed by the fishing club and Environment Agency (Dave Brady, *pers. comm.*). On the river bank there is evidence of scrub removal to make way for fishing but this has overgrown into swathes of nettle. There has recently been an in-river restoration project run by the head warden of the National Trust Blickling estate. The project aimed to 're-wild' sections of the Bure including the reach along the side of Mill Carr. It involved the selective felling of trees from the riverbank into the river to reinstate in-channel large wood structure that would naturally occur in rivers. This has left some tree stumps at the southern edge of this study site. Although the riverbank edge of the site has been more modified, further into the woodland there are sections carpeted in common bluebell *Hyacinthoides non-scripta* and numerous naturally fallen trees and rotting wood which suggest it has been untouched for a long time.

Figure 2.17 Mill Carr study site. Evidence of dead wood throughout the site suggests it has been left untouched for a long time. Taken in 2009.

Figure 2.18 Coppiced tree re-growth in Mill Carr. Taken in 2009.

Shepherd's Carr - SC - TG 171305

This woodland site (Figure 2.19) is also on the north side of the River Bure and is bordered by pasture of varying grazing densities; some is very heavily-grazed. The study site is small, so the fauna within may be considerably influenced by surrounding land use practices. The woodland has a thick canopy with slightly more open areas occurring towards the river's edge. The tree cover is very mixed, primarily composed of *Alnus glutinosa*, *Corylus avellana*, *Fraxinus excelsior* and *Quercus rober*, with some *Prunus padus* trees also growing within the site. There are numerous old drainage ditches throughout which were mostly dry during fieldwork. Towards the northern edge the soil is relatively dry, while the soil is saturated within 20 m of the river.

Historic maps suggest that SC has been wooded since pre-1880s. Currently it is left unmanaged, but the entrance to the study site has considerable evidence of disturbance and an old pheasant pen, which suggests this area was used for game stocking. The pen has long since been abandoned leaving a thick forest of nettles.

Figure 2.19 Shepherd's Carr Study site looking south into the site from the northern border.

Rough Pasture Carr - RPC - TG 174303

This woodland site is on the north bank of the River Bure (Figure 2.20). The study site area is part of a larger well established wet woodland so it is bordered by further woodland apart from on its northern side where a thin submerged ditch leads onto an under-grazed rush dominated meadow. To the south is the river Bure, beyond which lies part of Moorgate Meadow study site and further pasture land. The site is very wet; seepage channels drain through the site into the river, boggy pools fill the bases of fallen trees, and there are a few very old drainage ditches, which are also filled with boggy water. The tree cover over the site is dominated by *Alnus glutinosa* and *Fraxinus excelsior*, but a number of other trees are also present: *Betula pendula*, *Corylus avellana*, *Crataegus monogyna*, *Euonymus europaeus*, *Prunus padus*, *Prunus spinosa* and *Quercus robur*.

The site has historically been left as woodland since long before 1880. It is privately owned and the owner has no history of previous management. However, the presence of drainage ditches within the site suggests that this woodland has not been free from management.

Figure 2.20 Rough Pasture Carr study site from the south river bank looking north. This photo was taken in April 2009 when woodland leaf cover was still sparse. The reeds in the foreground are part of the main river channel and form a slow-moving backwater habitat.

Moorgate Meadow - MM - TG 172304

This site (Figure 2.21) is a semi-improved pasture meadow bordered by the river to the north, woodland to the south and west and further pasture to the east. The meadow, despite extensive grazing by cattle, is suggested to be of 'very good' botanical diversity (Ghullam & Ellis, 2006), with damp areas supporting wet meadow species interspersed with some areas of higher and drier ground supporting patches of gorse.

The meadow is owned by the National Trust and has been managed as floodplain pasture for decades. Historic maps confirm that it has been open ground since pre-1880s and such floodplain areas were traditionally used for cattle and sheep grazing.

Figure 2.21 Moorgate Meadow study site looking west. The River Bure is to the right of the picture and a ditch runs along the left.

Ingworth Bridge - IB - TG 192292

This site is a grassland site on the west bank of the River Bure as it flows south from Ingworth (Figure 2.22). It is predominantly surrounded by grassland but bordered to the east by the road bridge from Ingworth, to the south by an old flowing river channel, to the north by a drainage ditch and to the west by the new river channel. As suggested, the grassland is located between an old meandering channel of the River Bure and a new river course. The old river course is still in use and flows as part of the land drainage system, joining the new river 200m downstream of the site. Maps dating back to 1880s suggest that the new river channel pre-dates that period and would have been constructed to serve Ingworth Mill. The river in this area is widened and deepened with high banks; these are likely to have historically ensured that a headwater and minimum drop was maintained for Ingworth Mill to function. Consequently, the new river channel is largely disconnected with its floodplain here, however the old channel has shallower banks and wetter conditions are evidence on the east of the site with large patches of *Glyceria maxima*. The site is owned by the National Trust Blickling Estate who manage it by annual mowing in the late summer months to prevent a dense cover of thistle *Cirsium* spp. and common nettle *Urtica diocia*.

Figure 2.22 Ingworth Bridge study site on the River Bure, looking north. The new river channel is on the right of the photograph, with visible high banks leading onto the natural floodplain level. The old meandering river channel is on the far left of the photograph. Photo taken in early spring, 2009.

2.4.3 River Wissey

Alder Carr - AC - TF 836010

This woodland (Figure 2.23) is bordered to the north by meadows, to the east by a ditch and further meadows, to the south by the river and pasture on the other bank, and to the south-west by a road and ford crossing the River Wissey. The site is part of a vast MoD training area and is therefore inaccessible to the public. This site has also been designated as 'Out of Bounds for All Purposes' for MoD personnel (Ministry of Defence, 2006). It is part of a larger designated SSSI called Hooks Wells which is a collection of semi-natural river valley habitats that have developed as a result of a long period of stable, traditional management (Natural England, 2001). The alder carr, *Alnus glutinosa*, is described as notable for its rich ground flora of both woodland and shade-tolerant plants (Natural England, 2001). Additionally a carpet of *Sphagnum* mosses are established in part of the woodland which is indication of a stable water table (Natural England, 2001). A considerable number of springs and groundwater upwellings can be found to the north-west of the site in and around two ponds (Figure 2.23). These springs and ponds source two shallow channels that flow south-westerly through the woodland into the river at the south-eastern edge of the site. They create an island in the middle of the site. High water tables are found throughout the site creating a number of areas with standing or slightly flowing water.

The dominant trees within the forest are *Alnus glutinosa*, *Fraxinus excelsior* and *Acer pseudoplatanus.* A diverse number of tree species also contributed to the tree cover, including *Corylus avellana, Crataegus monogyna, Fagus sylvatica, Populus x canescens, Prunus padus, Quercus robur, Salix alba, Salix cinerea and Salix fragilis.*

Land use history of the site suggests that woodland dates back to pre-1880 and Natural England SSSI documents suggest that its management has been 'long and stable'. There is little evidence of recent management, although the riverbanks are slightly raised suggesting previous dredging, and a small open area dominated by nettles on the south-western edge of the site suggests selective clearing of the river bank in this section for fishing.

Figure 2.23 Alder Carr on the River Wissey, looking east along a side channel through the site. Groundwater springs can be seen as the chalk coloured patches within the water. The channel's source is chalk springs and uprisings at the north-east of the site. Taken in early April 2010 so the canopy is moderately open.

Chapter 3. Alpha diversity of beetle assemblages within chalk river floodplains: habitat and landscape context

3.1 Introduction

Estimates suggest that floodplain environments harbour over half of the UK's approximately 30,000 non-marine invertebrate species (Hammond, 1996), of which carabid and staphylinid beetles are the predominant non-aquatic families (Hammond, 1998; Lott, 2003). In natural floodplain environments, communities of these beetle families contain numerous wetland species that are specifically adapted to high water levels and regimes of regular disturbance events (Zulka, 1994; Hering & Plachter, 1997; Betz, 1999; Lott, 2001; Betz, 2002; Lott, 2003). For example, some staphylinid species of the *Stenus* tribe walk on the water surface in order to cross the small areas of open water on natural floodplains (Betz, 1999; Lott, 2003), while other *Stenus* species have widened tarsal segments and adhesive setae adapted for climbing plant stems in fen and marsh habitats (Betz, 2002). Some carabid species such as *Agonum thoreyi* (Carabidae) have been observed purposefully entering water to avoid potential danger (Lott, 2003) and several species of the *Bembidion* tribe, notably *Bembidion assimile,* can swim with their legs to escape (Joy, 1910; Lott, 2003).

Carabid beetles have shown sensitivity to anthropogenic changes in different habitats, although much of the literature has focused on agricultural landscapes (Niemela, 2001; Niemela *et al.*, 2002; Aviron *et al.*, 2005; Driscoll & Weir, 2005; Da Silva *et al.*, 2008; Gaublomme *et al.*, 2008; Liu *et al.*, 2010; Liu *et al.*, 2011; Brooks *et al.*, 2012). Floodplain environments have been subject to considerable levels of anthropogenic modifications (Purseglove, 1988; Newbold *et al.*, 1989; Tockner & Stanford, 2002), yet research into the influence of these changes on carabid and other beetle communities has been limited (Hammond, 1998; Paetzold *et al.*, 2008). In particular, limited attention has been focussed on staphylinid species, despite their highly specialised life

histories (Bohac, 1999; Hammond, 2003; Lott, 2009; Lott & Anderson, 2011), sensitivity to anthropogenic influences (Krooss & Schaefer, 1998; Golden & Crist, 2000; Dauber *et al.*, 2005; Clough *et al.*, 2007; Luo *et al.*, 2013) and dominance in the floodplain ground fauna (Hammond, 1998; Lott, 2001, 2003). These factors make staphylinid beetles, in combination with carabid beetles, particularly suitable for assessing the influence of anthropogenic modifications and in estimating the success of conservation and restoration measures in floodplain habitats (Boscaini *et al.*, 2000; Niemela, 2001; Rainio & Niemelä, 2003; Günther & Assmann, 2005). In addition, due to the high number of rare and stenotopic carabid and staphylinid species (Hyman & Parsons, 1992; Drake, 1998; Hammond, 1998; Lott, 2003) and a general decline in abundances of some groups (Brooks *et al.*, 2012), carabid and staphylinid beetles themselves may become targets for conservation efforts.

Alpha (α-) diversity, that is the richness of taxa within a site or habitat (Whittaker, 1960, 1965, 1972; Sepkoski, 1988; Magurran & McGill, 2011a), has been widely used in biodiversity assessments. α-diversity encompasses both *species richness*, that is a simple measure of the number of species sampled in a habitat, and dominance and evenness of different species within habitat, which is incorporated into *α-diversity indices* (Magurran, 2004). Species richness and α-diversity indices have often been used to assess the state of habitats (e.g. Tockner *et al.*, 1999; Martikainen *et al.*, 2000; Magura, 2002; Sabo *et al.*, 2005), the impact of anthropogenic modifications on ecosystems (e.g. Weibull *et al.*, 2003; Woodcock *et al.*, 2005a; Lövei *et al.*, 2006), and used as a tool to measure the effectiveness of restoration and enhancement of ecosystems (Ruiz-Jaen & Mitchell Aide, 2005). Although species richness and α-diversity indices reduce down a large volume of data to one value thereby providing only a high-level overview of the biodiversity within a habitat (Jeanneret *et al.*, 2003a), they offer a suitable index with which to compare the diversity of species between different habitats and habitat states.

England hosts the largest number of chalk rivers in Europe (Environment Agency, 2004). These rivers have been subject to substantial anthropogenic modifications (Smith *et al.*, 2003; Environment Agency, 2004), and whilst the effects of these modifications on in-stream biota and biodiversity have been widely studied (e.g. Wood & Petts, 1999; Harrison & Harris, 2002; Smith *et al.*, 2003), little attention has been focused towards biodiversity on chalk river floodplains. Information is therefore urgently needed on the biodiversity of these habitats to assist with conservation and restoration practices.

This chapter addresses these needs by investigating the α-diversity of carabid and staphylinid beetles on the floodplains of three chalk rivers in Norfolk eastern England. It tackles the following four questions: (1) How alpha-diverse are beetle assemblages on UK chalk river floodplains? (2) Are the floodplain habitats of these chalk rivers differentiated by the α-diversity of beetle assemblages they support? (3) What are the dominant site and landscape factors influencing beetle α-diversity? (4) Do carabid and staphylinid beetles show similar α-diversity patterns in floodplain environments?

3.2 Methodology

3.2.1 Field methods

Fifteen study sites were chosen from the Rivers Glaven (n = 9), Bure (n = 5) and Wissey (n=1) (Table 2.2) to represent the dominant land use types on the floodplain environments of these chalk rivers. A total of five meadows, three fens and seven woodland sites were selected to enable comparison across habitat types and catchments. All floodplain sites were located in the middle reaches of the three rivers (Figure 2.2). Section 2.4 outlines full contemporary and historical information for the study sites.

Beetle sampling

To characterise seasonal and inter-annual variation in beetle assemblage, field collections were undertaken between April and September in 2009 and 2010. Samples were collected using five replicate 2 x 2 m plots randomly distributed throughout each study site at a minimum distance of 10 m from each other to ensure spatial sample independence. Beetles were sampled using two unbaited pitfall traps per plot, separated by 1 m (Figure 3.1). The limitations of pitfall trapping have been emphasised (Spence & Niemelä, 1994 and references therein), yet this method remains simple and effective for standardised ground dwelling arthropod sampling, allowing for comparability across sites (Apigian *et al.*, 2006). Catch sizes from pitfall traps indicate 'activity density', that is a function of both beetle movement on the soil surface and population density (Lester & Morrill, 1989). Beetles must be active, or they will not encounter the traps. Species abundance and diversity is referred to in this chapter with the knowledge that pitfall trap catches represent 'activity-density' (Baars, 1979; Niemalä *et al.*, 1990; Apigian *et al.*, 2006; Woodcock & Pywell, 2009). However, any

sample bias towards more active species is likely to be consistent within and between sites, allowing for their direct comparison (Greenwood *et al.*, 1991).

Figure 3.1 Dimensions of each plot and images of pitfall traps and covers

For pitfall trap placement, holes were dug into the substrate using a corer, and plastic cups of 75 mm diameter and 100 mm depth were placed into the holes. Traps were placed level or slightly below the level of the substrate surface to avoid deterring beetles with the cup lips (Woodcock, 2005), but in areas of severe waterlogging, difficulties arose due to surface water entering and flooding the traps. In these cases, these traps were excluded from analyses. Each trap was half filled with a preservative solution of 50% industrial methylated spirit (IMS) and 50% water, with a drop of detergent added to break the surface tension. There have been discussions of the attraction of different preservatives in pitfall traps (e.g. Luff, 1968; Holopainen, 1990). However, preservative was essential to stop samples decaying during week-long sampling periods and has been commonplace in pitfall sampling methods. A non-obstructing cover was placed approximate 40 mm above the ground to protect traps from litter fall and rain (Figure 3.1). The traps were set for 7 days at a time, four times each year between April and September (Table 3.1). Table 3.2 shows a summary of collected beetle samples from the 15 study sties. Alder Carr, a highly pristine floodplain woodland on military land, was located in 2010. Access to the site was negotiated, which enabled a full dataset to be obtained for the 2010 field season.

Table 3.1 Timings of 7-day beetle sampling in 2009 and 2010

Collection	2009 collection	2010 collection
1	28 May – 4 June	13 May- 20 May
2	20 July - 26 July	18 June - 25 June
3	20 August - 26 August	21 July - 28 July
4	21 Sept - 28 Sept	27 August - 4 Sept

Table 3.2 Study site success for beetle collections. '-' represents no samples for that collection and was caused by inaccessibility to sites. '' means that one quadrat has been missed due to inaccessibility or water logging.*

	Site Name	Site Code	2009				2010			
			1	2	3	4	1	2	3	4
Meadow	Hunworth Castle	HCA	✓	✓	-	-	✓	✓	✓	✓
	Hunworth Railway	HR	✓	✓	✓	✓	✓	✓	-	-
	Hunworth Meadow	HM	✓	✓	✓	✓	✓	✓	✓	✓*
	Moorgate Meadow	MM	✓	-	-	✓	✓*	✓*	-	-
	Ingworth Bridge	IB	✓	✓	-	✓	✓	✓	-	✓
Fen	Holt Lowes Fen	HLF	✓	✓	✓	✓	✓	✓	-	-
	Glaven Farm	GF	✓	✓	✓	✓	✓	✓	✓	✓
	Wildflower Fen	WF	✓	✓	✓	✓	✓	✓	✓	✓
Woodland	Holt Lowes Woodland	HLW	✓	✓	✓	✓	✓	✓	✓	✓
	Hunworth Woods	HW	✓	✓	✓	✓	✓	✓	✓	✓
	Wildflower Woods	WW	✓	✓	✓	✓	✓	✓	✓	✓
	Mill Carr	MC	✓	✓	✓	✓	✓	✓	✓*	✓*
	Shepherd's Carr	SC	✓	✓	✓	✓	✓	✓	✓*	✓*
	Rough Pasture Carr	RPC	✓	✓	✓	✓	✓	✓	✓	✓
	Alder Carr	AC	-	-	-	-	✓	✓	✓	✓

Beetle identification

Beetles were sorted and identified to species level using Joy (1932), Tronquet (2006), Luff (2007), Lott (2009) and Lott and Anderson (2011). No special light source was used although specimens were carefully manipulated to study beetle micro-sculpture. Distinction between staphylinid species often relied upon differences in genitalia rather than external characteristics; as such, staphylinid beetles were frequently dissected (Figure 3.2). When difficulties arose in identification of certain specimens, reference collections at the British Entomological and Natural History Society (BENHS) were used in the first instance. Any uncharacteristic species, or species new to an area, were checked and confirmed with the Norfolk County Coleopteran Recorder, Martin Collier, or by the former Natural History Museum's Coleopteran curator, Dr Peter Hammond.

A number of similar species were grouped, as they are chiefly separable using male genitalia, which only permits the identification of male specimens. For carabid species, these were *Pterostichus nigrita* and *Pterostichus rhaeticus*, which were grouped into *Pterostichus nigrita* agg. For staphylinid species, *Anotylus sculpturatus* and *Anotylus mutator* were grouped into *Anotylus sculpturatus* agg., and *Quedius curtipennis* and *Quedius fuliginosus* were combined as *Quedius fuliginosus* agg. Some female specimens of *Gabrius* spp. and *Stenus* spp. (Staphylinidae) were not identified and excluded from

the analysis, as a number of species in these genera can again only be distinguished by the male genitalia.

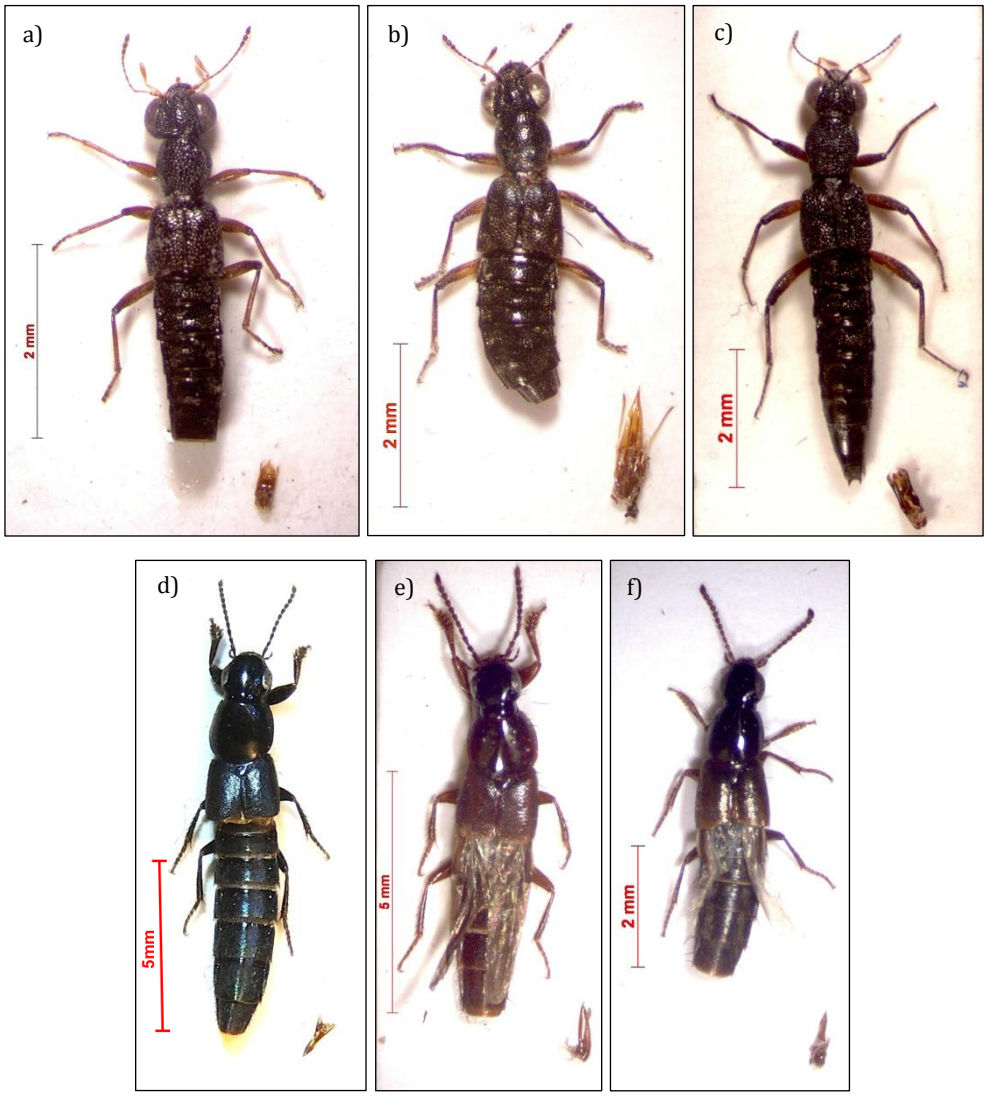


Figure 3.2 Examples of dissected specimens of Stenus *spp. and* Quedius *spp. with their genitalia (bottom right of each picture): a)* Stenus aceris*, b)* Stenus nitidiusculus*, c)* Stenus providus*, d)* Quedius fuliginosus*, e)* Quedius humeralis*, and f)* Quedius schatzmayri.

Members of the *Aleocharinae* subfamily of Staphylinidae were not identified to species level. As with the above, species in this sub-family can generally only be distinguished by their genitalia, leaving female specimens indistinguishable. This is particularly true of the genus *Atheta,* within which many species can coexist in a given habitat (Sawada, 1972). Unfortunately, given the considerable size of this subfamily, difficulty in the identification and dissection of such small specimens, the time required for dissection and the potential exclusion of large numbers of female specimens, specimens were combined as *Aleocharinae* spp. and excluded from subsequent analyses.

Recording of vegetation, other site parameters and landscape characteristics

Vegetation species richness was recorded within 2 x 2 m quadrats, and percentage cover estimated for each species of vascular plant present. Plants were identified to species level using identification guides by Hubbard (1984), Rose *et al.* (2006) and Jermy *et al.* (2007). Cover estimates were recorded in 5% intervals, however 1% intervals were used for cover estimates between 1 and 5%. Vegetation was sampled in May-June 2009, with further notes taken of newly appearing species throughout April-September 2009-2010 during beetle trapping.

To evaluate the effects of site and landscape factors on beetle α-diversity, a series of site and landscape descriptors were defined (Table 3.3). Site dimensions (area, perimeter, edge density) were calculated from Ordnance Survey maps using EDINA Digimap online software (EDINA, 2012). The Shannon α-diversity index was calculated to characterise the diversity of the vegetation at each site (equation in Table 3.5). Surrounding land use within a 250 m radius was estimated using EDINA and aerial photographs, which provided percentage cover values for different land uses. This approach was followed to focus on the effects of the neighbouring landscape, while investigations of wider landscape effects were not feasible within the scope of this study. In addition to land use type composition, a landscape pattern index was calculated to quantify the surrounding landscape arrangement for each site and to capture the major features of landscape pattern such as heterogeneity and dominance. The index D_1 measures the extent to which land use types dominate the landscape, by using the Shannon α-diversity index on measures of surrounding land use (O'Neill *et al.*, 1988: Table 3.3). A full table of site and landscape characteristics for the 15 floodplain sites is given in Appendix 2.

Table 3.3 Site and landscape characteristics considered for each site.

Scale	Environmental Variable	Description
Site descriptors	Habitat type	Meadow, fen, woodland
	Site area	Area of site in (m^2)
	Vegetation cover	Percentage cover of vegetation
	Grazing	Scale of grazing intensity: 0- no grazing; 1- temporary/light grazing; 2- heavy grazing.
	Cutting	Vegetation cutting 0- no cutting; 1- cut once a year
Landscape descriptors	River	Glaven, Bure, Wissey
	Perimeter	Site Perimeter (m)
	Edge density (ED)	Perimeter to area ratio: $ED = \frac{E}{A}$, where E is the total edge or perimeter (m), and A is the area (ha)
	Landscape pattern index (D_1)	D_1 is a landscape index that measures dominance of land use types (O'Neill *et al.*, 1988; Jeanneret *et al.*, 2003b): $D_1 = \ln n + \sum p_i \ln p_i$ where n is the total number of land use types and p_i is the proportion of patches in land use i. All surrounding land uses were considered for this index.
	Surrounding arable land (SA)	Percentage of arable land surrounding site within a 250 m radius
	Surrounding woodland (SW)	Percentage of woodland surrounding site within a 250 m radius
	Surrounding meadow (SM)	Percentage of meadow surrounding site within a 250 m radius

3.2.2 Statistical analysis

Species richness estimation

The large number of beetle species found at relatively small spatial scales means a complete measurement of species richness is seldom, if ever, achieved (Colwell & Coddington, 1994; Brose, 2002). As such, a number of methods have been established to account for this. Non-parametric species estimators such as Chao1 and Chao2 use information of rare species in samples to extrapolate a hypothetical value that adjusts for those species present on the site but not contained in the actual sample, thereby providing an estimate of the complete species richness of an area or assemblage collection (Gotelli & Colwell, 2001; Magurran & McGill, 2011b). Although estimates can vary significantly between estimator and are subject to large confidence intervals for small datasets, such variances are said to be 'inevitable' as the estimator metrics

represent extrapolation beyond the limits of the collected data (Magurran & McGill, 2011b).

A number of non-parametric estimators have been calculated to provide estimates of species richness for each site (Table 3.4). Chao1 uses abundance data to estimate species richness as a function of the ratio of singletons (observed species that are represented by a single individual) and doubletons (observed species that are represented by two individuals) (Colwell & Coddington, 1994; Magurran, 2004). Chao2 uses incidence data based on the number of unique species in each sample and those occurring in only two samples. Both Chao1 and Chao2 were used in their bias-corrected form, which takes into account unequal or small sample sizes (Colwell, 2009). Jacknife species estimators also use incidence based data; Jacknife1 uses unique species (Burnham & Overton, 1978, 1979) while Jacknife2 uses both the number of unique species and the number of species found in two samples (Smith & van Belle, 1984). The Bootstrap estimator is related to the Jacknife approach; with incidence data, the proportion of quadrats containing each species with a resampling procedure is used to estimate species richness (Efron, 1979; Smith & van Belle, 1984).

Brose (2002) tested the efficiency of certain non-parametric estimators in carabid communities in order to evaluate the sampling effort required for insect species diversity studies and found Chao2 to be the most accurate and precise estimator. In another study of arthropods in isolated pasture lands, Borges and Brown (2003) found Jacknife1 and Chao1 to generate larger estimates of species richness while Bootstrap provided lower estimates. General reviews of species estimators have provided little consensus on which procedure is best (Colwell & Coddington, 1994; Hellmann & Fowler, 1999; Apigian *et al.*, 2006). For that reason, an arithmetic mean of Chao1, Chao2, Jacknife1, Jacknife2 and Bootstrap estimators , named S_{true}, was calculated for each site similar to Brose (2002) to provide a more robust estimate of total species richness. Species estimators were all calculated using EstimateS 8.2.0 (Colwell, 2009).

Table 3.4 Species estimators calculated for each site. Formulae are based on Magurran (2004) and Colwell (2009).

Estimator	Formulae
Chao1 Bias Corrected (abundance data)	$S_{Chao1} = S_{obs} + \left(\frac{n-1}{n}\right)\frac{F_1(F_1-1)}{2F_2(F_2+1)}$ Where S_{obs} is the number of species in the sample; n is the number of individuals; F_1 is the number of singletons; F_2 is the number of doubletons.
Chao2 Bias Corrected (incidence data)	$S_{Chao2} = S_{obs} + \left(\frac{m-1}{m}\right)\frac{Q_1(Q_1-1)}{2(Q_2+1)}$ Where m is the number of samples; Q_1 is the number of species that occur in one sample only (unique species); Q_2 is the number of species that occur in two samples.
Jacknife1	$S_{Jack1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right)$
Jacknife2	$S_{Jack2} = S_{obs} + \left(\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right)$
Bootstrap	$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}}(1-p_k)^m$ Where p_k is the amount of samples containing species k.

α-diversity indices

Rather than the simple count of the number of species, α-diversity indices can capture a measure of both richness and evenness characteristic of an assemblage (Magurran, 2004) with the aim of eliminating the influence of sample size (Rosenzweig, 1995). To explore difference in α-diversity of beetle communities between habitat types, three diversity indices were calculated: Shannon's H, Simpson's D and Fisher's α (Table 3.5). The Shannon or Shannon-Wiener diversity index combines species richness with relative abundance and calculates entropy of 'chaos' in the distribution. The Simpson's index takes into account both the number of species present and the abundance of each species, and measures the probability that two individuals randomly selected from a sample will belong to the same species. For both, Jost (2006) suggests transformations to account for true diversity rather than an index (equations in Table 3.5). Fisher's α is a parametric index of diversity that assumes that the abundance of species follows the log series distribution. It has been proven to be widely sample-size independent and a reliable measure of diversity (Fisher *et al.*, 1943; Kempton & Taylor, 1974; Kempton &

Wedderburn, 1978; Axmacher *et al.*, 2004a; Axmacher *et al.*, 2004b; Axmacher *et al.*, 2008; Liu *et al.*, 2011). As pitfall trapping represents activity density rather than species density, Fisher's α is considered to be a robust measure to calculate species diversity for this method of sampling (Axmacher *et al.*, 2011; Liu *et al.*, 2011).

Table 3.5 α-diversity indices calculated for each site. Formulae based on Magurran (2004).

Estimator	Formulae
Shannon's H	$H = -\sum p_i \ln p_i$ Where p_i = the number of specimen i/total specimens. Transformation into true diversity as recommended by (Jost, 2006): $\exp(-\sum p_i \ln p_i)$.
Simpson's D	$D = 1/\sum {p_i}^2$ Where p_i = the number of specimen i/total specimens.
Fisher's Alpha	$S = \alpha \ln\left(1 + \frac{n}{\alpha}\right)$ Where S is the number of species, n is the number of individuals and α is Fisher's α.

Correlations between the three measured diversity indices were calculated, along with tests of normality of the data using QQ-plots and Shapiro Wilk tests, to assess which index provided the most suitable description of the data's α-diversity. The index correlated with other indices and showing a normal distribution was then used in all further analysis.

Comparison of species richness and diversity indices

To ascertain if significant diversity differences existed between habitat types, one-way analysis of variance (ANOVA) was calculated for estimated species richness (S_{true}) and the chosen α-diversity index. ANOVA assumes a normal distribution, which was checked using the Shapiro Wilk test prior to analysis. Significance levels for all tests were set at $p<0.05$. These were displayed using boxplots.

α-diversity and environment relationships

All habitat and landscape variables were tested for normal distributions using Shapiro-Wilk tests and QQ-plots and variables were transformed where needed. Pearson's Product-Moment Correlations were calculated to provide an initial assessment of the relationships between α-diversity measurements and site and landscape factors.

α-diversity and environment relationships were further explored using multiple linear regressions. The α-diversity measures (S_{true} and α-diversity index) for carabid and staphylinid beetles were used individually as dependent parameters against habitat and landscape characteristics. General linear regression models were defined using a combination of forward and backward selection procedures to ensure that the most suitable model was identified. Model quality was tested using Akaike's Information Criterion (AIC), which is based on goodness of fit (high constrained inertia), but penalises for the number of predictor parameters included (Bozdogan, 1987; Oksanen, 2011). Multi-collinearity was accounted for by ensuring correlated variables such as area, perimeter and edge density were not incorporated together in the final model. If significantly correlated variables also predicted beetle α-diversity significantly, the parameter best predicting α-diversity as indicated by the most significant correlation with this factor was selected in place of others. To address the problem associated with a small sample size (one calculation for each site), permutation tests (critical $p<0.01$; 9999 permutations) were used on final models using the 'lmPerm' package in R (Wheeler, 2010). Permutation tests also provide an additional means of confirming selection of appropriate model variables (González-Megías *et al.*, 2008).

Species indicator values

Indicator species analysis was carried out to determine whether certain species were characteristic to certain habitat types or management practices. Indicator species can be used to determine the preference of species to certain habitat conditions, often represented in sampled data by classified groups (McGeogh, 1998; De Cáceres *et al.*, 2010). The indicator value approach (IndVal) was used (Dufrene & Legendre, 1997; De Cáceres *et al.*, 2010), which is based on an indicator value index to measure specificity and fidelity. Specificity is based on the association between species and a site group using abundance data, whereas fidelity is based on the presence and absence of that species in different, pre-defined categories of sites. Most suitable indicator species are those that are abundant in a specific site or group and predominantly found in only those sites, resulting in high values for both specificity and fidelity. For this analysis, the significance of associations was tested using random permutations. The analysis was carried out using the 'indicspecies' package in R (De Cáceres & Legendre, 2009; R Development Core Team, 2011).

Table 3.6 Summary of analytical methods used in Chapter 3

Analytical Method	Application
Species richness estimation	To provide estimates of species richness for each site, accounting for species present the site but not contained in the actual sample.
α-diversity indices	To provide comparable measurements of α-diversity for sites, and explore the suitability of three commonly used α-diversity indices (Shannon's H, Simpson's D and Fisher's α) for floodplain beetle assemblages.
One-way analysis of variance (ANOVA)	To ascertain if significant α-diversity differences existed between habitat types.
Pearson Product-Moment Correlations	To provide an initial assessment of the relationships between α-diversity measurements and site and landscape factors
Multiple linear regression	To assess the combined influence of site and landscape factors on beetle assemblages.
Species Indicator Values	To determine whether certain species were characteristic to certain habitat types or management practices

3.3 Results

Abundance

A total of 8727 carabid and staphylinid beetles were collected in 2009 and 2010 (Table 3.7), of which 8060 were positively assigned to one of 142 species. A species list and abundances by habitats is given in Tables 3.8 and 3.9. Notable species include the carabid beetle *Agonum piceum*, found at Wildflower Fen (WF), which is rare to Norfolk (Luff, 1998, M.Collier pers. comm.), and the staphylinid beetle *Erichsonius signaticornis* found at Glaven Farm (GF), which is most commonly found on exposed sand and shingle near rivers and the known species distribution is restricted to south west England, north-west England and some parts of Scotland (Lott & Anderson, 2011).

Table 3.7 Summary of carabid and staphylinid specimens collected from 15 chalk floodplain sites in 2009 and 2010.

	2009 Collections	2010 Collections
Carabid beetles	2029	1100
Staphylinid beetles	2002 (226 *Aleocharinae*)	3596 (385 *Aleocharinae*)
Yearly Totals	4031	4696
Total	**8727**	

Table 3.8 Total carabid species' abundances grouped by habitat.

	Habitat		
Species	**Woodland**	**Fen**	**Meadow**
Elaphrus cupreus	22	-	-
Cychrus caraboides	13	-	-
Leistus fulvibarbis	12	-	-
Calathus rotundicollis	6	-	-
Stenolophus teutonus	6	-	-
Trechus quadristriatus	5	-	-
Abax parallelepipedus	1	-	-
Amara ovata	1	-	-
Bembidion dentellum	1	-	-
Bembidion quadrimaculatum	1	-	-
Patrobus atrorufus	527	-	19
Carabus granulatus	403	-	104
Pterostichus madidus	87	-	24
Notiophilus biguttatus	21	-	1
Bembidion tetracolum	1	-	1
Pterostichus nigrita agg.	394	105	45
Nebria brevicollis	305	2	5
Pterostichus niger	138	32	117
Pterostichus minor	71	18	5
Loricera pilicornis	60	5	1
Carabus nemoralis	43	3	6
Pterostichus melanarius	25	1	10
Pterostichus strenuus	21	6	43
Bembidion mannerheimii	11	3	31
Agonum emarginatum	10	12	7
Pterostichus diligens	5	41	37
Agonum fuliginosum	1	39	18
Agonum piceum	-	6	-
Agonum thoreyi	-	4	-
Acupalpus parvulus	-	1	-
Agonum micans	-	1	-
Bembidion assimile	-	1	-
Clivina collaris	-	1	-
Stenolophus mixtus	-	1	-
Anisodactylus binotatus	-	2	19
Poecilus versicolor	-	1	36
Acupalpus dubious	-	1	8
Harpalus rufipes	-	1	4
Bembidion guttula	-	-	36
Amara communis	-	-	32
Pterostichus vernalis	-	-	25
Agonum viduum	-	-	2
Amara lunicollis	-	-	2
Bembidion lampros	-	-	2
Bembidion obtusum	-	-	2
Clivina fossor	-	-	2

Agonum muelleri	-	-	1
Amara familiaris	-	-	1
Anchomenus dorsalis	-	-	1
Blemus discus	-	-	1
Bradycellus harpalinus	-	-	1
Poecilus cupreus	-	-	1
Stomis pumicatus	-	-	1

Table 3.9 Total staphylinid species' abundances grouped by habitat

	Habitat		
Species	**Woodland**	**Fen**	**Meadow**
Proteinus brachypterus	30	-	-
Quedius fumatus	19	-	-
Tasigus morsitans	18	-	-
Olophrum piceum	14	-	-
Omalium rivulare	14	-	-
Carpelimus elongatulus	12	-	-
Lesteva longoelytrata	10	-	-
Bisnius fimeratus	9	-	-
Quedius picipes	8	-	-
Ocypus brunnipes	5	-	-
Othius punctulatus	5	-	-
Stenus binotatus	5	-	-
Coprophilus Striatulus	4	-	-
Micropeplus staphylinoides	4	-	-
Tasigus melanarius	4	-	-
Rugilus rufipes	3	-	-
Stenus nitidiusculus	3	-	-
Stenus picipes	3	-	-
Bolitobius cingulatus	2	-	-
Carpelimus erichsoni agg	2	-	-
Lesteva punctata	2	-	-
Othius subuliformis	2	-	-
Stenus impressus	2	-	-
Stenus lustrator	2	-	-
Lathrobium fovulum	1	-	-
Lathrobium longulum	1	-	-
Omalium caesum	1	-	-
Quedius lateralis	1	-	-
Quedius scintillans	1	-	-
Stenus aceris	1	-	-
Tachinus humeralis	1	-	-
Tachyporus chrysomelinus	1	-	-
Staphylinus erythropterus	24	65	-
Lathrobium fulvipenne	3	5	-
Oxytelus fulvipes	44	-	2
Gabrius breviventer	12	-	12
Philonthus marginatus	9	-	5
Philonthus laminatus	3	-	5

Xantholinus linearis	2	-	9
Philonthus tenuicornis	2	-	3
Ocypus aeneocephalus	2	-	2
Quedius nicriceps	2	-	1
Stenus pusillus	1	-	3
Mycetoporus lepidus	1	-	2
Tachyporus hypnorum	1	-	1
Tachinus rufipes	900	59	654
Anotylus rugosus	551	533	476
Philonthus decorus	427	1	4
Stenus bimaculatus	146	30	48
Quedius maurorufus	53	38	26
Quedius fuliginosus	48	20	29
Lathrobium brunnipes	43	9	13
Anotylus sculpturatus agg	41	1	6
Tachinus marginellus	13	4	12
Lesteva heeri	11	2	5
Stenus providus	8	2	12
Gabrius trossulus	4	12	5
Stenus juno	4	5	18
Philonthus intermedis	4	1	5
Ischnosoma splendidum	3	3	2
Xantholinus longiventris	3	2	15
Quedius nemoralis	2	2	2
Quedius molochinus	1	9	22
Ocypus olens	1	1	1
Lathrobium terminatum	-	3	-
Paederus riparius	-	3	-
Erichsonius signaticornis	-	1	-
Lathrobium geminum	-	1	-
Metopsia clypteata	-	1	-
Stenus clavicornis	-	3	1
Tachyporus dispar	-	1	27
Philonthus succicola	-	1	10
Rugilus erichsonii	-	-	43
Philonthus cognatus	-	-	27
Stenus fulvicornis	-	-	8
Philonthus varians	-	-	7
Quedius schatzmayri	-	-	7
Quedius semiobscurus	-	-	5
Rugilus orbiculatus	-	-	4
Othius angustus	-	-	3
Philonthus carbonarius	-	-	2
Quedius boops	-	-	2
Quedius nitipennis	-	-	2
Stenus solutus	-	-	2
Carpelimus corticinus	-	-	1
Quedius levicollis	-	-	1
Sepepophilus marshami	-	-	1
Tachinus solutus	-	-	1

Beetle abundances varied considerably between sites, ranging from 656 staphylinids at Ingworth Bridge to 95 at Moorgate Meadow, the latter of which was affected by considerable cattle disturbance (see Table 3.2). The highest number of carabid specimens were found at Rough Pasture Carr (n=629), while the lowest specimen counts originated from Hunworth Woods (n=36).

Carabid samples were dominated by five species; *Patrobus atrorufus, Pterostichus nigrita* agg.*, Carabus granulatus, Nebria brevicollis* and *Pterostichus niger.* Together, these species accounted for 70% of all carabid specimens collected. Two staphylinid species dominated the trap collections: *Tachinus rufipes* and *Anotylus rugosus.* Together, they accounted for 64% of all staphylinid specimens. Some 16 carabid and 17 staphylinid species were singletons, i.e. only represented by one individual when all samples were combined.

Estimated species richness varied considerably between species diversity estimators for some sites (a full table of estimated species richness results can be found in Appendix 3). For example, at HLW, the Chao1 calculation estimated total staphylinid species richness to be 45, Jacknife2 as 54 and Chao2 at 61. A comparison of the observed species richness (S_{obs}) and the arithmetic mean of all calculated estimators (S_{true}) (Figure 3.3) indicated that the sampling regime resulted in a sampling completeness between 64-93% for carabid beetle species and 62-85% of staphylinid beetle species, suggesting that collection efforts did not fully sample the respective species richness. S_{obs} was consistently higher for staphylinids than carabids in all but two sites, where it was equal (WF: 20 species; HR: 22 species). Similarly, S_{true} was also higher for staphylinids in all sites apart from the same two sites, where carabid S_{true} was higher (WF: S_{true} carabids – 28.74, S_{true} staphylinids – 24.32; HR: S_{true} carabids – 32.17, S_{true} staphylinids – 26.58).

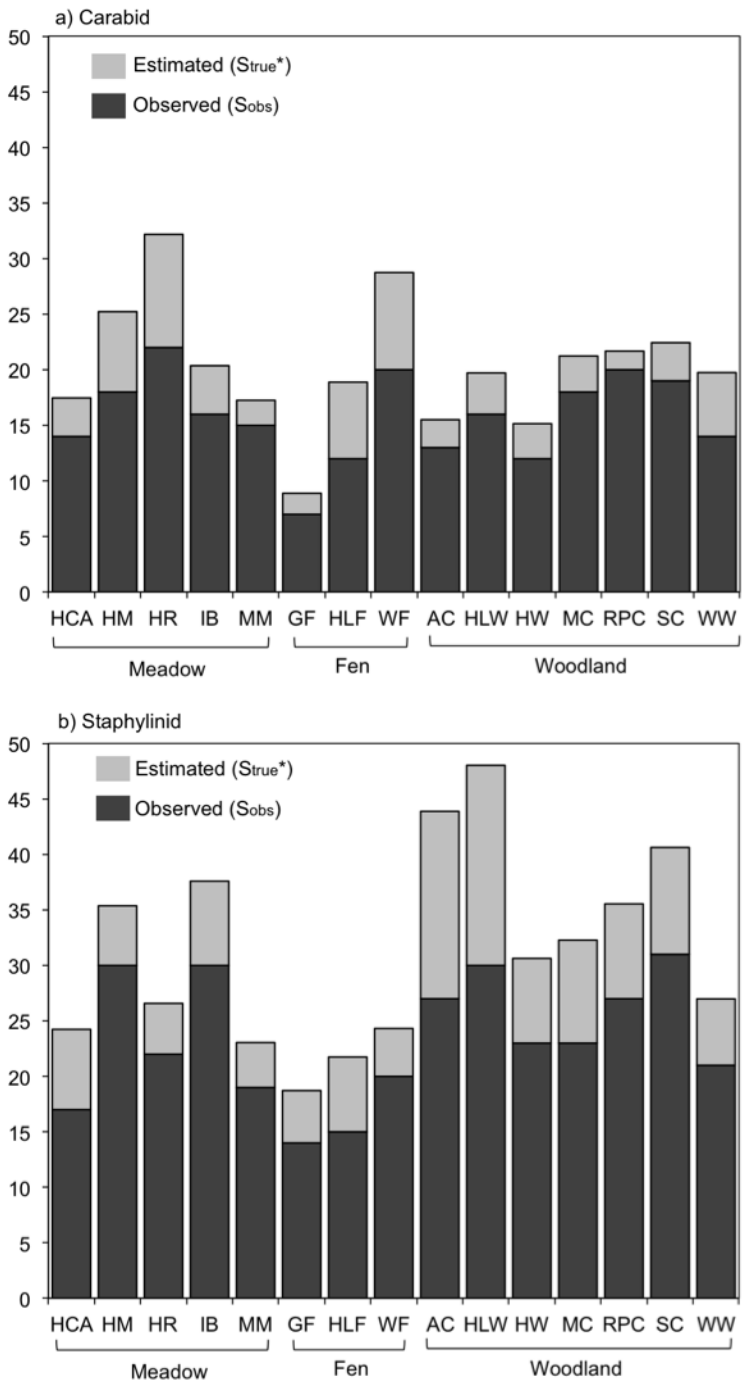


Figure 3.3 Observed species richness (S_{obs}) and estimated total species richness (S_{true*}) for each site. Full tables showing Chao1, Chao2, Jacknife1, Jacknife2 and Bootstrap estimator calculations can be found in Appendix 3. Sites are abbreviated according to Table 2.2.

Fisher's α, Shannon Wiener and Simpson's α-diversity indices showed significant correlations (R>0.715, p<0.01 in all cases; a full table of α-diversity index results can be found in Appendix 4). QQ-plots and Shapiro Wilk tests showed Fisher's α to be the most normally distributed. In addition to this, the sample-size independence of Fisher's α means it is considered the most suitable index and will hence be exclusively used in all further analysis. A test for the relationship between Fisher's α and estimated species richness detected significantly positive correlations for both carabid and staphylinid beetles (R=0.47, p=0.04; R=0.81, p<0.01, respectively; Figure 3.4).

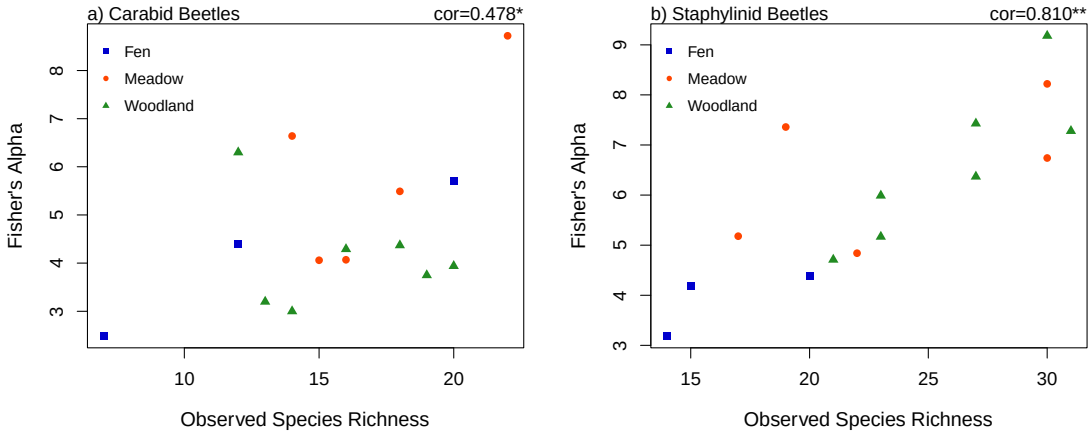


Figure 3.4 Relationship between the chosen α-diversity index (Fisher's α) and observed species richness for carabid and staphylinid beetles. S_{true} was not used here as Fisher's α was calculated using observed species not estimated species

Between habitat comparisons (Figure 3.5) revealed no significant differences for carabid and staphylinid abundances ($F_{2,12}$=2.74, p=0.10; $F_{2,12}$=0.45, p=0.65, respectively), carabid species richness or carabid Fisher's α ($F_{2,12}$=0.54, p=0.60 and $F_{2,12}$=1.98, p=0.18, respectively). Whereas, staphylinid species richness and Fisher's α were both significantly different (p<0.05) between habitats ($F_{2,12}$=5.73, p=0.02; $F_{2,12}$=4.32, p=0.04, respectively). Meadow habitats harboured the most species rich communities and were the most α-diverse habitats for both carabids and staphylinids, whereas fen habitats provided the least diverse communities, particularly for staphylinids.

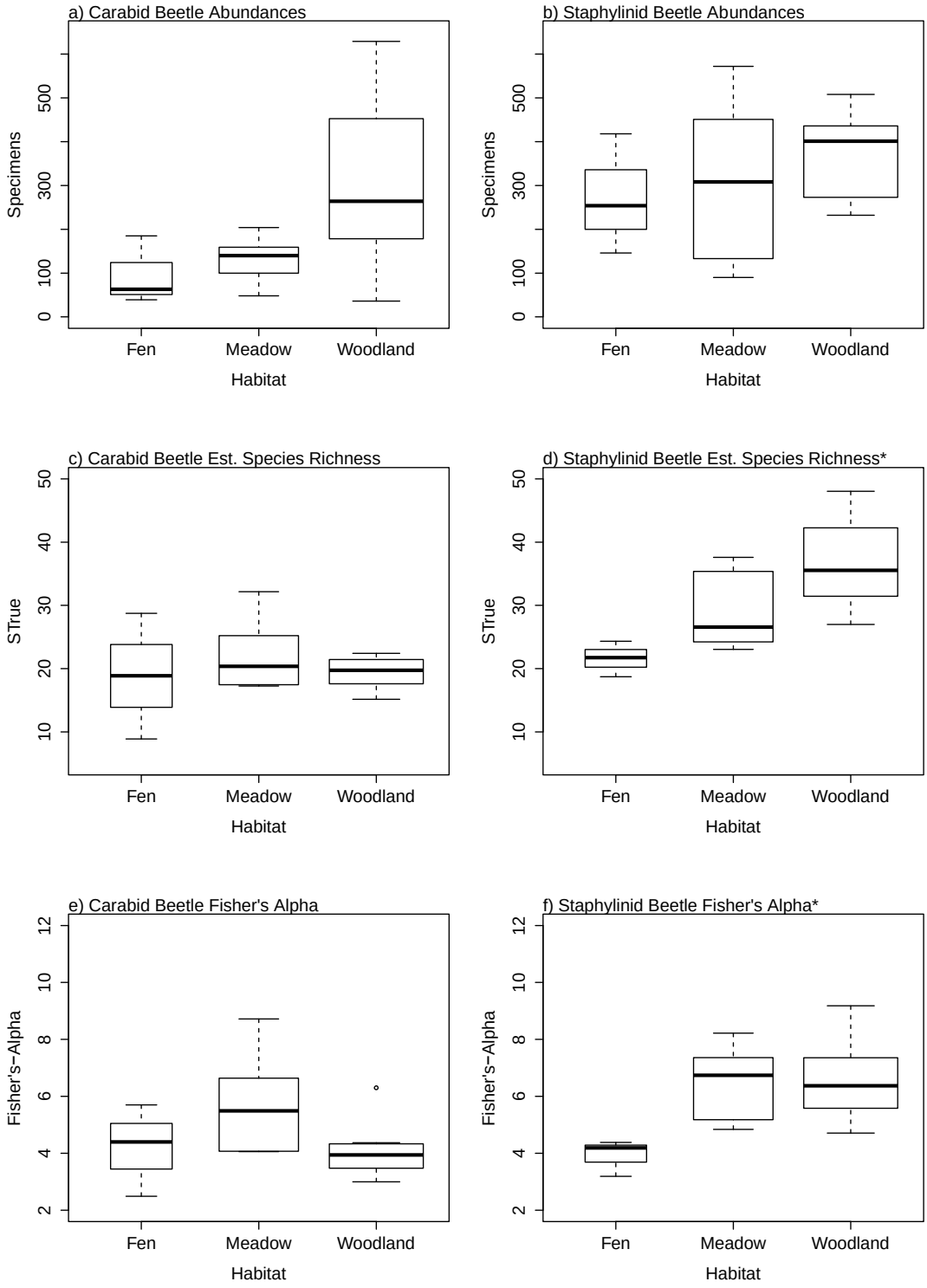


Figure 3.5 Comparisons of beetle abundances, estimated species richness and Fisher's α between habitat types. S_{true} is the arithmetic mean of Chao1, Chao2, Jacknife1, Jacknife2 and Bootstrap estimators. Significant relationships ($p<0.05$) were found between staphylinid beetle species richness and Fisher's α.

Influence of site and landscape factors on α-diversity

No significant relationship was found between carabid species richness any habitat and landscape variables, whereas carabid Fisher's α was significantly related to grazing (R=0.54, p=0.05; Table 3.10). Significant relationships were identified between staphylinid species richness and site area, perimeter, vegetation species richness, and vegetation cover (R=0.56, p=0.04; R=0.56, p=0.04; R=-0.59, p=0.03; and R=-0.76, p<0.01, respectively). Fisher's α of staphylinid beetles was also significantly correlated with vegetation species richness and vegetation cover (R=-0.58, p=0.03; R=-0.65, p=0.01, respectively).

*Table 3.10 Pearson correlations between site and landscape factors and beetle α-diversity. S_{true} is the arithmetic mean of Chao1, Chao2, Jacknife1, Jacknife2 and Bootstrap estimators. Significant calculations are shown in bold displayed, significance is shown as '**' <0.01, '*' <0.05.*

	Correlation Coefficient			
	Carabidae		**Staphylinidae**	
	S_{true}	**Fisher's α**	**S_{true}**	**Fisher's α**
Site Descriptors				
Area	0.12	-0.21	**0.56***	0.35
Vegetation species richness	0.37	-0.42	**-0.59***	**-0.58***
Vegetation α-diversity	0.18	-0.38	-0.36	-0.27
Vegetation cover	0.28	0.42	**-0.76****	**-0.65****
Grazing	0.29	**0.54***	-0.06	0.18
Cutting	-0.43	-0.37	-0.18	-0.24
Landscape Descriptors				
Perimeter	0.17	-0.07	**0.56***	0.42
Edge density	-0.08	0.43	-0.48	-0.21
Landscape pattern index (D_1)	0.07	0.40	-0.22	0.02
Surrounding arable land (SA)	0.47	0.24	-0.23	-0.04
Surrounding meadow (SM)	0.10	0.14	0.34	0.05
Surrounding woodland (SW)	0.01	-0.05	0.13	0.18

Multiple linear regression models indicated that different combinations of habitat and landscape factors explained staphylinid and carabid α-diversity in the study areas (Table 3.11). In correspondence to the Pearson correlation results, no significant explanatory variables were identified predicting estimated carabid species richness, and grazing was the only significant variable to influence estimated carabid species richness (adjusted R^2=0.23, p=0.05, Table 3.11). Vegetation had the most dominant influence on both staphylinid species richness and α-diversity; vegetation richness and

vegetation cover were selected by forward selection models as best explanatory factors for staphylinid Fisher's α (adjusted R^2=0.51, p<0.01), while vegetation cover, richness and surrounding meadow were selected for staphylinid estimated species richness (adjusted R^2=0.69, p<0.01).

Table 3.11 Regression models for carabid and staphylinid α-diversity measures.

Beetle α-Diversity	Model				Model Parameters		
	Adj. R^2	F	p	AIC	Predictor Variables	Beta	p
S_{true}							
Carabidae	No significant model						
Staphylinidae	0.69	10.75	<0.01	48.01	Vegetation cover	-0.16	<0.01
					Vegetation richness	-0.45	<0.01
					Surrounding meadow	1.44	0.18
Fisher's α							
Carabidae	0.23	4.95	0.05	12.53	Grazing	1.81	0.04
Staphylinidae	0.51	7.65	<0.01	7.59	Vegetation richness	-0.03	0.03
					Vegetation cover	-0.10	0.06

Indicator species

Indicator species analysis revealed a larger number of potential indicator species in staphylinid than in carabid beetles, reflecting their higher overall abundances and species richness. Five carabid species were indicative of specific habitats (Table 3.12), although fidelity to those habitats was not high in any of these cases. Similarly, 13 staphylinid species were indicative of specific habitats (Table 3.13), but again with low fidelity values. The results suggest that *Staphylinus erythropterus* was indicative of fen habitats, but the indicator statistic was not high as it was primarily found at one site, Holt Lowes Fen. This species is a heathland specialist species, suggesting it might have migrated into this habitat from surrounding heathland in the Holt Lowes SSSI. *Rugilus erichsonii* and *Tachyporus dispar* (Staphylinidae) were indicators of meadow habitats, while high abundances of *Philonthus decorus*, *Proteinus brachypterus*, *Anotylus sculpturatus* agg. and *Oxytelus fulvipes* (Staphylinidae) were linked to woodland habitats.

No species were indicative of un-grazed sites, but one carabid (*Carabus nemoralis*) and two staphylinids (*Staphylinus erythropterus* and *Olophrum piceum*) characteristically occurred on grazed sites. Two carabids (*Pterostichus vernalis* and *Amara communis*) and four staphylinids (*Rugilus erichsonii*, *Tachyporus dispar*, *Philonthus cognatus*, and *Stenus fulvicornis*) were furthermore characteristic of heavily grazed sites. Finally, two carabid species (*Amara communis* and *Bembidion guttula*) and three staphylinid

species (*Tachyporus dispar, Tachinus marginellus* and *Stenus juno*) were characteristic of cut sites.

*Table 3.12 Carabid indicator species for habitats, grazed sites and cut sites. 'A' represents the IndVal statistic for specificity and 'B' represents the IndVal statistic for fidelity. 'Stat' represents the overall indicator statistic. Significance is shown as '**' p <0.01, '***' p<0.001 Due to the number of species, indicator species were only considered significantly different if p < 0.01.*

		Carabidae			
Factor	**Category**	**Species**	**A**	**B**	**Stat**
Habitat	Fen	-	-	-	
	Meadow	*Pterostichus vernalis****	1.00	0.44	0.66
		*Amara communis****	1.00	0.28	0.53
		*Anisodactylus binotatus***	0.93	0.28	0.51
		*Poecilus versicolor***	0.98	0. 24	0.49
	Woodland	*Cychrus caraboides***	1.00	0.23	0.48
		*Leistus fulvibarbis***	1.00	0.23	0.48
Grazing	Un-grazed	-			
	Grazed	*Carabus nemoralis****	0.92	0.50	0.68
	Heavily grazed	*Pterostichus vernalis****	1.00	0.44	0.66
		*Amara communis **	1.00	0.28	0.53
Cutting	Uncut	*Pterostichus nigrita* agg. ***	0.95	0.83	0.89
	Cut	*Amara communis ****	0.97	0.50	0.70
		*Bembidion guttula ****	0.99	0.30	0.55

*Table 3.13 Staphylinid indicator species for habitats, grazed sites and cut sites. 'A' represents the IndVal statistic for specificity and 'B' represents the IndVal statistic for fidelity. 'Stat' represents the overall indicator statistic. Significance is shown as '**' p <0.01, '***' p<0.001 Due to the number of species, indicator species were only considered significantly different if p < 0.01.*

		Staphylinidae			
Factor	**Category**	**Species**	**A**	**B**	**Stat**
Habitat	Fen	*Staphylinus erythropterus* **	0.86	0.33	0.54
	Meadow	*Rugilus erichsonii* ***	1.00	0. 72	0.85
		Tachyporus dispar ***	0.94	0.44	0.64
		Philonthus cognatus ***	1.00	0. 36	0.60
		Stenus fulvicornis **	1.00	0.28	0.53
	Woodland	*Philonthus decorus* ***	0.98	0.91	0.95
		Proteinus brachypterus ***	1.00	0. 49	0.70
		Anotylus sculpturatus agg. **	0.79	0. 46	0.60
		Oxytelus fulvipes **	0. 94	0. 34	0.57
		Quedius fumatus **	1.00	0.31	0.56
		Olophrum piceum **	1.00	0. 26	0.51
		Lesteva longoelytrata **	1.00	0.23	0.48
		Omalium rivulare **	1.00	0.23	0.48
Grazing	Un-grazed	-			
	Grazed	*Staphylinus erythropterus* ***	1.00	0.90	0.95
		Olophrum piceum **	0.84	0.40	0.58
	Heavily grazed	*Rugilus erichsonii* ***	1.00	0.72	0.85
		Tachyporus dispar **	0.92	0.44	0.64
		Philonthus cognatus **	1.00	0.36	0.60
		Stenus fulvicornis **	1.00	0.28	0.53
Cutting	Uncut	-			
	Cut	*Tachyporus dispar* **	0.93	0.50	0.68
		*Tachinus marginellus***	0.71	0.60	0.65
		Stenus juno **	0. 89	0.40	0.60

3.4 Discussion

3.4.1 Floodplain beetle α-diversity

As transitional ecotones between terrestrial and aquatic habitats, floodplains characteristically support high levels of biodiversity (Junk *et al.*, 1989; Naiman *et al.*, 1993; Naiman & Décamps, 1997; Ward *et al.*, 1999; Robinson *et al.*, 2002; Tockner & Stanford, 2002). Accordingly, levels of staphylinid species richness identified within the River Glaven, Bure and Wissey sites were high (89 species overall with a maximum of 31 species at single sites), and although there are few comparable floodplain studies, these species numbers, which also excluded *Aleocharinae* species, were relative to

other floodplain studies for example on the River Trent, UK (Greenwood *et al.*, 1991) and on Romanian rivers (Stan, 2011; Table 3.14). Levels of carabid species richness (53 species in total and up to 22 per site) are comparable to numbers recorded for example on the Trent, Adige-Noce (Italy) and Garonne rivers (France) (Greenwood *et al.*, 1991; Boscaini *et al.*, 2000), while more speciose communities have been found in other European floodplain habitats. Many floodplain habitats in central Europe have been subject to less intensive management, with some large sections of naturally flooded habitats still preserved (Adis & Junk, 2002). Their floodplains have been shown to host high numbers of carabid species and sometimes harbour high numbers of extremely rare wetland carabid species (Zulka, 1994). The River Elbe and Oder in Germany are examples of this, as they host relatively natural floodplain habitats including patches of endangered alluvial *Quercus–Ulmus* forests that support a high species richness of carabids (Bonn *et al.*, 2002, Table 3.14).

Table 3.14 Selection of European floodplain beetle studies.

Reference	**Location**	**Carabid Species Richness**	**Staphylinid Species Richness**
This Study	River Glaven, UK River Bure, UK River Wissey, UK	7-22 per site 15-20 per site 13 per site (53 over 15 sites)	14-30 per site 19-31 per site 27 per site (89 over 15 sites)
Greenwood *et al.* (1991)	River Trent, UK	11-25 per site	5-31 per site
Boscaini *et al.* (2000)	River Trent UK Adige-Noce, Italy Garonne, France	58 over 15 sites 56 over 15 sites 70 over 15 sites	
Bonn *et al.* (2002)	River Elbe, Germany River Oder, Germany River Weser, Germany	99 over 12 sites 157 over 23 sites 102 over 10 sites	
Baiocchi *et al.* (2012)	River Aniene and its tributaries, Italy	52 over 45 sites	
Stan (2011)	Rivers Danube, Buzău, Prut and Râmnica Sărat, Romania		94 over 23 sites

Traditionally managed fen habitats have also been shown to support high levels of diversity (Middleton *et al.*, 2006; McBride *et al.*, 2011) and harbour a number rare beetle species (Hammond, 1998). However, within this research, floodplain fens showed uncharacteristically low levels of α-diversity. This may be, in part, attributable to management legacies, as these sites have been subject to multiple management practices over the course of decades and even centuries. The fen at Glaven Farm is now

managed using traditional fen management practices, but the site was once a pig farm. Wildflower Fen has had inconsistent management over the past fifty years and additionally Holt Lowes Fen was historically set aside as common land for grazing and small plots of crops (site profiles are outlined in Chapter 2). The presence and distribution of species is closely linked to environmental and biotic legacies in floodplain landscapes (Robinson *et al.*, 2002). Harding *et al.* (1998) assert that the loss of species in aquatic environments is attributable to land use fifty years previously rather than within the last decade, and that agriculture in particular can result in long-term reductions in species diversity, regardless of current habitat and management types. While the plant diversity of these fen sites was characteristically high, historic influences may have had a stronger impact on beetle communities for which the (re-) establishment of any habitat specialist species is chiefly dependent on natural immigration (Woodcock & McDonald, 2010). This colonisation may lag behind plant species colonisation, particularly when these fen habitats are positioned in a highly fragmented landscape. Such historic legacies may be a contributing factor to the low diversity and lack of fen-specific indicator species found in the fen habitats on the River Glaven.

Furthermore, the small size of the fen habitats may have reduced their ability to support species-rich beetle communities. The theory of island biogeography (MacArthur & Wilson, 1967) outlines that as habitat areas increase in size, they can provide an increasing number and type of resources and niches for species to exploit and therefore support a higher number of species. Empirical evidence for this theory was demonstrated within this study by staphylinid species richness, whereby habitats of larger sizes supported higher numbers of species. The relationship is commonly non-linear, and thresholds exist for populations, below which certain species do not persist (With & King, 1999; Fahrig, 2001; Fahrig, 2003, Figure 3.6). The relationship is also dependent on the isolation and spatial arrangement of the remaining habitat within the landscape (With & King, 1999; Ewers & Didham, 2007). In combination with site history, the small size (all under 4000 m^2) and isolation of the fen have reduced their ability to support species-rich beetle communities.

Historic influences and habitat extent may in part help to explain the low diversity in fen habitats and therefore may, in part, explain the lack of significant differences identified between habitats, yet this latter finding may also be related to the α-diversity measurements themselves. Similar species richness values in different habitats can still be related to significantly different species assemblages (Jeanneret *et al.*, 2003a), as

any measures in turnover or β-diversity are obviously not taken into account in these values. The indicator species analysis captured this variation, highlighting that there were indeed a number of different species indicative of meadow and woodland habitats, and of grazing and cutting management practices, confirming that although α-diversity measurements may not be significantly different, the communities these values represent may be distinct.

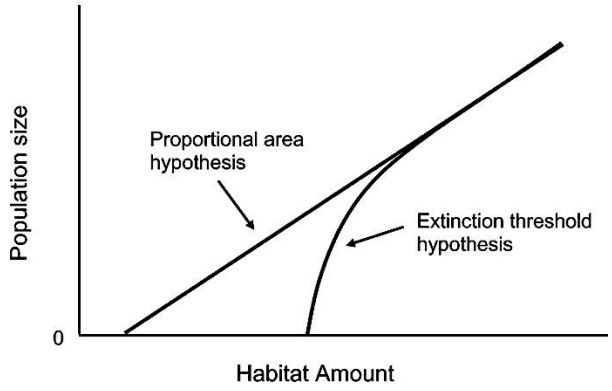


Figure 3.6 Illustration of the extinction threshold hypothesis in comparison to the proportional area hypothesis from Fahrig (2003), which demonstrates the theoretical threshold of habitat amount (size) below which populations cannot persist.

3.4.2 Influence of site and surrounding landscape characteristics on beetle α-diversity

The contribution of vegetation to staphylinid α-diversity was marked in these floodplain habitats. The negative relationships demonstrated for vegetation cover and vegetation species richness contrasts with two relevant ecological theories. The first, the 'taxonomic diversity hypothesis', suggests that the taxonomic diversity of plant species is positively correlated with the diversity of herbivores and further predators within the food chain, as each additional type of resource can have specialised consumers (Murdoch *et al.*, 1972; Hunter & Price, 1992; Prendergast *et al.*, 1993; Siemann, 1998; Siemann *et al.*, 1998; Brose, 2003a). The second theory, the 'structural/habitat heterogeneity hypothesis', assumes that structurally complex habitats may provide more niches and ways of exploiting resources and therefore promote higher diversity of organisms (Southwood *et al.*, 1979; Tews *et al.*, 2004). However, neither hypothesis considers the importance of bare ground, which is a notable habitat feature for beetles, for hunting prey, warmth, excavating burrows, and

ease of movement (Key, 2000). Results in this study correspond to previous studies exemplifying the large number of staphylinid species that have been shown to inhabit less well vegetated riverine areas in high numbers, including numbers of rare and habitat specific species (Andersen, 1983; Key, 2000; Eyre *et al.*, 2001a; Eyre *et al.*, 2001b; Blake *et al.*, 2003). The concept that bare ground can be important habitats for beetle species yet botanically unexceptional is important for biodiversity conservation, which often uses plant diversity as a positive surrogate for other taxa. Furthermore, the contrasting results between beetle families within this study and throughout the literature suggest that the relationship between beetles and vegetation is by no means simple. Rather, correspondence between vegetation and beetle diversity may be more strongly related to edaphic factors to which both communities are responding (Andersen, 1983; Gardiner, 1998; Bonn & Kleinwächter, 1999; Blake *et al.*, 2003). However, the detection of both direct relationships in correlations and multiple linear regressions shows there is a strong underlying correlation in the investigated floodplain environments for staphylinid beetles, regardless of the facilitating mechanism.

Although carabid α-diversity was not related to vegetation *per se*, grazing was shown to influence carabid species richness. Grazing is one of the main management practices used to maintain the faunal quality of fen habitats (Middleton *et al.*, 2006; McBride *et al.*, 2011) and calcareous grassland (Woodcock *et al.*, 2005a). This management prevents vegetation from becoming dominated by a few vigorous plants and provides an element of structural diversity as cattle graze selectively (McBride *et al.*, 2011). Dunging and trampling also influence the plant composition of the sward. The subsequent structural heterogeneity and mosaic of different microhabitats can provide more combinations of resources to satisfy the contrasting requirements of different species and therefore increase the diversity of assemblages (Dennis *et al.*, 2002). This relationship has been demonstrated for both carabid and staphylinid beetles (Murdoch *et al.*, 1972; Dennis *et al.*, 1997; Brose, 2003a; Woodcock *et al.*, 2006). However, the relationship has also been shown to be species specific and in addition related to stocking densities (Dennis *et al.*, 1997). Notably, in agreement with indicator species results, *Staphylinus erythropterus*, found primarily in Holt Lowes Fen, has been associated with lower stocking densities and higher vegetation height, and *Olophrum piceum* has also been associated with grazed sites (Dennis *et al.*, 1997, Figure 3.7).

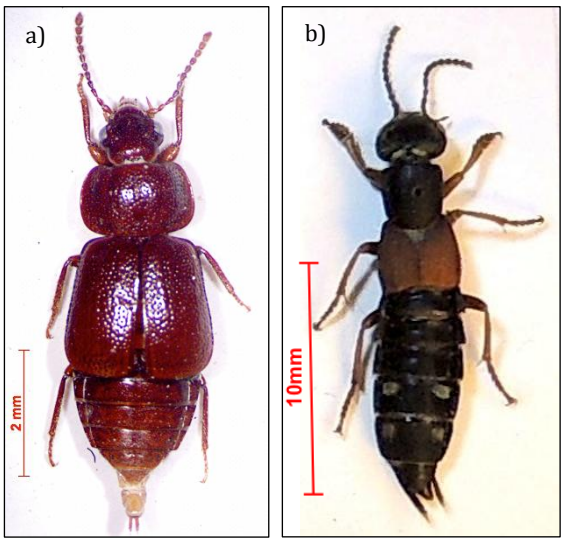


Figure 3.7 Staphylinid specimens: a) Olophrum piceum *and b)* Staphylinus erythropterus. *Both species were associated with grazed floodplain meadows and fens within this study and in previous research (Dennis et al., 1997).*

As suggested, area can contribute to higher beetle species richness in accordance to the island biogeography theory (MacArthur & Wilson, 1967). However, within terrestrial landscapes, habitat 'islands' or patches are typically surrounded by less hostile environments than the island biogeography theory suggests. These terrestrial habitats often host their own set of beetle species, which influence the diversity of the focal patch (Cook *et al.*, 2002; Lövei *et al.*, 2006). A higher perimeter means increasing influence from the surrounding habitats, and the positive relationships between staphylinid species richness and both perimeter and surrounding meadow identified within this study suggests that species from the surrounding landscape do indeed exert an influence on the α-diversity of staphylinids within these sites. Carabid and staphylinid species richness has been shown to increase with increasing ratios of perimeter to area due to higher colonisation rates and migratory influx from species originating in surrounding habitats (e.g. Golden & Crist, 2000; Magura, 2002). However, similar to grazing, this relationship varies between species (Ewers & Didham, 2008; Rykken *et al.*, 2011) and generalist species are often favoured by high perimeter to area ratios (Niemela, 2001; Gaublomme *et al.*, 2008). Small forest patches with resulting high edge densities have been shown to support particularly high numbers of generalist species (Lövei *et al.*, 2006). Edge effects might therefore have reduced the overall individuality in the species pools and diversity of the different habitat types and may hence have contributed to the similar levels of α-diversity across the habitat types within this study.

3.4.3 Conservation implications

Beetles in floodplain ecosystems

Carabid and staphylinid beetles play essential roles in the functioning of ecosystems (Bouchard *et al.*, 2009; Schuldt & Assmann, 2010); in their predatory role on aphids and springtails, and as decomposers of algae, fungi and decaying organic matter (Good & Giller, 1991). In particular in floodplain ecosystems they have a significant role in linking aquatic and terrestrial food webs (Paetzold *et al.*, 2005) and as prey for riparian birds (Hagar *et al.*, 2012). However, the significance of carabid and staphylinid species on floodplains is commonly understated (Lott, 2003), and there has been a distinct lack of attention to the species diversity of carabid and staphylinid beetles in floodplain environments (Hammond, 1998; Paetzold *et al.*, 2008). This chapter has provided insight into the α-diversity patterns of these families within a range of chalk floodplain habitats. The results suggest that despite the levels of anthropogenic disturbance within and around these habitats, some habitat patches still support a highly diverse array of beetle species, comparable to more pristine habitats along rivers in central Europe. In particular, the results highlight the high diversity of staphylinid beetle assemblages in comparison to carabid assemblages (staphylinids regularly displayed higher species richness and α-diversity across all habitat types). There are more than double the number of staphylinid species associated with wetland habitats in comparison to carabids due to the predominant hygrophilous or mesophilous habitat requirements of staphylinids (Lott, 2003). Although both beetle families in general are often overlooked in floodplain biodiversity and conservation surveys which commonly focus primarily on plant species, staphylinid beetles in particular have been widely neglected (Lott, 2009; Lott & Anderson, 2011). This study confirms that staphylinid assemblages are speciose in a range of chalk river floodplain environments, provide a strong indication of habitat management and should not be ignored in floodplain research and conservation management.

The results suggest that staphylinid α-diversity is influenced by different environmental factors to carabid beetles. Other studies have also shown that diversity patterns can strongly diverge between different insect taxa (Holloway *et al.*, 1992; Usher *et al.*, 1993; Lawton *et al.*, 1998; Niemelä & Baur, 1998; Weibull *et al.*, 2003; Diekotter *et al.*, 2008; Axmacher *et al.*, 2011). This study, along this growing body of research, demonstrates that evaluation of habitats for conservation using species richness of a single surrogate taxa, even if it represents similar ecological traits like carabids as potential surrogates of staphylinids, may not suitably represent the

biodiversity of the other taxa (Oliver *et al.*, 1998; Weibull *et al.*, 2003). Furthermore, a lack of consistent relationship between insect assemblages and vegetation, demonstrated here with the different responses of carabid and staphylinid α-diversity to vegetation, and again identified in a growing body of literature (e.g. Oliver *et al.*, 1998; Blake *et al.*, 2003; Brose, 2003a; Schuldt *et al.*, 2009; Schuldt & Assmann, 2010; Axmacher *et al.*, 2011), highlights the risks in many current approaches of biodiversity conservation that commonly use vegetation-based surrogates to assess the overall status and trends in biodiversity (Woodcock & McDonald, 2010; Axmacher *et al.*, 2011).

Investigating beetle α-diversity

It is evident that a number of different factors influence beetle α-diversity, yet, correlations and relationships presented within this study were obviously dependent on the α-diversity measurement considered. The results within this chapter suggest that the site and landscape factors may influence different components of overall α-diversity within these communities. For example area and perimeter were shown to influence staphylinid species richness but not Fisher's α. Different metrics are known to measure different aspects of α-diversity (Buckland *et al.*, 2005). α-diversity indices including Fisher's α not only capture species richness, but in parallel provide a measure of evenness within a sample (Magurran, 2004). The results within this study suggest that the evenness and dominance addressed by Fisher's α is most impacted by vegetation composition. By contrast, species richness alone was influenced by habitat area and perimeter in addition to vegetation variables. This highlights the importance of understanding community structure in biodiversity conservation, rather than simply focussing on the number of species present in a habitat (Magurran & Henderson, 2003).

A concern that arises from the variation in response of the metric used is that the choice of α-diversity measurement used for conservation studies and practices have potentially strong implications for the resulting diversity patterns. The difference in performance of the species estimation metrics within this study was apparent. Conservation and restoration practices often use and require a metric or metrics to compare habitats, habitat stages and restoration success (Ehrenfeld, 2000; Coscaron *et al.*, 2009; Woodcock & McDonald, 2010), as it is virtually impossible to obtain complete inventories of species prior and post management, particularly in highly diverse and dynamic habitats such as floodplains (Naiman *et al.*, 1993; Naiman & Décamps, 1997; Tockner & Stanford, 2002) and for highly diverse and mobile insect taxa (Coscaron *et*

al., 2009). As outlined within the methodology of this paper, a plethora of α-diversity indices have been developed to account for different aspects of α-diversity (see Magurran, 2004). The choice of metric in many scientific studies and applied conservation evaluation is often directed by data availability and in some cases by experimenting with regards to which metric shows the strongest environmental relationships (Beck *et al.*, 2013). However, *a priori* consideration for which aspect of diversity is relevant for the study objective (Yoccoz *et al.*, 2001), and the suitability of certain metrics for the organism in question (Brose & Martinez, 2004) is essential. Shannon's diversity or entropy has been widely used to summarise plant α-diversity, for highly mobile species, particularly where trapping is dependent on activity patterns, more sample-size independent metrics such as Fisher's α may be more suitable (Axmacher *et al.*, 2011; Liu *et al.*, 2011).

Conservation of floodplain habitats

Although only a significant distinction was identified for staphylinid α-diversity between habitat types, meadow habitats showed consistently highest diversity levels for carabid and staphylinid beetles in comparison to woodland and fen habitats. Lowland wet grasslands, which includes floodplain meadows, are known to have a high nature conservation value (Fuller, 1987; Jefferson & Grice, 1998; Gowing *et al.*, 2002), yet to date there has been a lack of research into invertebrate assemblages associated with this habitat (Drake, 1998; Woodcock *et al.*, 2006). Meadows are characteristically species rich in grasses and herbs, and traditional grazing or cutting practices prevent domination of swards by one or a few species (Rodwell, 1992). This plant species richness provides diverse habitats for invertebrates in terms of structure, cover and food sources, and consequently these environments support a heterogeneous combination of microhabitats that species can utilise during different stages in their life cycle (Benstead *et al.*, 1997; Drake, 1998). These include tussock-forming rushes and grasses important for over-wintering carabid beetles, litter layers of varying depths which provide habitat for beetle prey, and bare ground important for basking, feeding, excavation of burrows and courtship of carabid and staphylinid beetles (Benstead *et al.*, 1997; Key, 2000). Additionally, hedgerows and rough field margins that typically surround meadows can further enhance species diversity by providing shelter, sources of litter and prey (Luff, 1996; Benstead *et al.*, 1997; Drake, 1998). The significance of managed meadow habitats for beetle α-diversity within the context of this research confirms the importance of managed habitats in addition to remaining remnants of natural habitat.

The importance of consistent management has been highlighted for fen habitats. Drainage, conversion to intensive agricultural use, abstractions and lack of management have reduced the number and size of these environments throughout the UK (Hammond, 1998; Maddock, 2008). Despite the uncharacteristically low beetle species richness on the three fen sites studied within the context of this research, fen-specific species were still present in Wildflower Fen, notably *Agonum piceum*, a rare stenotopic carabid fen species rare to Norfolk (M. Collier pers. comm.), other fen-associated carabid species such as *Acupalpus parvulus*, *Agonum fuliginosum*, *Agonum thoreyi* and *Bembidion assimile* (Luff, 1998; Lott, 2003; Luff, 2007; Figure 3.8) and the staphylinid species *Gabrius trossulus*, *Paederus riparius*, and *Quedius maurorufus* (Lott, 2003; Lott & Anderson, 2011). The persistence of these fen species highlights firstly the ability of even small fen patches to host some characteristic fen species, and secondly the importance to conserve even small patches of this habitat throughout the landscape using suitable and traditional management practices, not only for the populations hosted within but to help link and maintain a metapopulation structure for fen communities by providing 'stepping stones' through which fen species can disperse (Hammond, 1998).

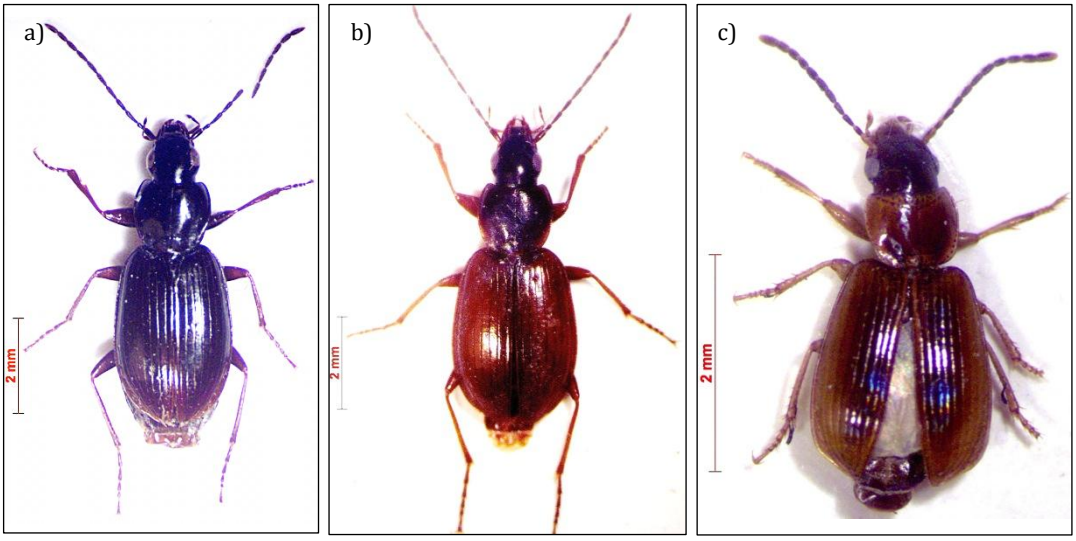


Figure 3.8 Carabid specimens: Agonum fuliginosum, Agonum piceum *(a rare fen species in Norfolk), and* Acupalpus parvulus*. All are associated with fen habitats and were found in Wildflower Fen on the River Glaven.*

This may also be true for natural floodplain woodlands, which are generally considered to be more invertebrate rich than floodplain grasslands (Adis & Junk, 2002) and form the natural vegetation cover expected in European floodplain habitats. Research has shown that a number of stenotopic floodplain beetles have been lost from British

floodplain woodlands (Buckland & Dinnin, 1993), and the fauna associated with natural UK floodplains would most likely have been larger and contained more specialist species than the communities found in remnant and fragmented areas of semi-natural floodplain forest today (Drake & Sheppard, 1998). While remarkable levels of beetle α-diversity were not found in these environments, unlike relatively undisturbed examples of these woodlands in Central Europe (Zulka, 1994; Bonn *et al.*, 2002), high abundances were recorded within woodland sites, in particular for carabid beetles. While considering that abundances from pitfall traps represent activity density and not true densities, this suggests that these habitats can support high numbers of active beetles. Anthropogenic disturbance has been found to negatively affect the abundance of carabid beetles (e.g. Alaruikka *et al.*, 2002), and the lower levels of disturbance within woodland habitats may enable a higher number of specimens to establish themselves. Additionally, the results of indicator species analysis suggest that these floodplain woodland habitats still host the highest number of indicator species, particularly in staphylinids. Similar to fen habitats, high abundances of these specialist species may be important to help maintain metapopulation of woodland specialists by proving refuge and dispersal stepping stones.

Floodplain and river landscapes are made up of a complex mosaic of habitat types, including meadows, fens and woodlands that vary in space and over time as a result of both natural and anthropogenic forces. Species richness across multiple habitats (gamma diversity) is a product of the species richness of each constituent patch (α-diversity) and the turnover of species between these patches (beta diversity) (Ward *et al.*, 1999; Ballinger *et al.*, 2007). Landscapes made up of a mosaic of habitats have been shown to host higher diversity even if patches vary in species richness themselves (Da Silva *et al.*, 2008). Despite the differing levels of α-diversity identified within this study, including the low α-diversity of fen habitats, the different communities that they represent and different abundances they can support suggest that a combination of habitat types in these floodplain landscapes promotes higher gamma diversity within the landscape. Therefore conservation of different habitat types should be an essential part of a wider catchment conservation perspective.

3.5 Conclusion

In summary, this chapter has addressed the critical prevailing lack of information about beetle biodiversity in chalk river floodplains. The influence of management practices, habitat extent and vegetation on beetle alpha diversity confirms that anthropogenic changes have altered the biodiversity of these landscapes. Furthermore the low diversity of fen habitats in particular suggests that anthropogenic influences, including land use change, inconsistent management and habitat fragmentation, may have reduced the ability of fen habitats to high α-diversity communities for which they are known. However, the presence of specialist species in fen habitats and high beetle abundances in floodplain woodlands highlights the importance of conserving these habitat patches.

Though α-diversity measurements can provide an initial assessment of the conservation needs and restoration importance, they do not adequately reflect variations in species compositions (Scott & Anderson, 2003). Additional analysis of the community composition within these floodplain habitats is needed to reveal further evidence about the dominant factors influencing these chalk floodplain beetle communities.

Chapter 4. Beta diversity of beetle assemblages within chalk-river floodplains: habitat and landscape context

4.1 Introduction

As already highlighted in previous chapters, there is an increasing need to investigate biodiversity within floodplain habitats, attempt to quantify the impact of anthropogenic modifications, and inform conservation practices. Species alpha (α-) diversity measurements can provide useful estimates and metrics to describe both species richness and evenness within habitats for conservation consideration (e.g. Greenwood *et al.*, 1991; Bonn *et al.*, 2002; Apigian *et al.*, 2006; Axmacher *et al.*, 2011), but they provide no indication of community composition. In contrast, beta (β-) diversity is a measure of the variation in species composition between localities or habitats (Whittaker, 1972), and represents the differentiation component of biodiversity rather than the inventory component (McKnight *et al.*, 2007). β-diversity patterns are the result of complex interaction of species' ecological traits with characteristics of the physical landscape over time (Baiocchi *et al.*, 2012), operating simultaneously and across a range of spatial and temporal scales (Whittaker *et al.*, 2001; Dauber *et al.*, 2005; Hendrickx *et al.*, 2007). β-diversity patterns therefore represent an appropriate method to assess the current biodiversity of floodplain landscapes, and quantify the responses and sensitivity of communities to environmental change (Duelli *et al.*, 1999; Jeanneret *et al.*, 2003a; Hendrickx *et al.*, 2007).

Both site and landscape factors have been shown to influence beetle community composition (e.g. Thiele, 1977; Gutzwiller, 2002; Brose, 2003a; De La Peña *et al.*, 2003; Weibull *et al.*, 2003; Lassau *et al.*, 2005; Hendrickx *et al.*, 2007). Whilst site factors such as management can influence the habitat structure and resources available for species (e.g. Morris, 2000; Woodcock *et al.*, 2005a; Middleton *et al.*, 2006), landscape factors

are becoming more widely recognised in highly fragmented landscapes as communities are increasingly exposed to influence from the surrounding habitat matrix (Cook *et al.*, 2002). The composition and spatial arrangement of the landscape can affect the local recruitment of species from the regional pool (Lawton, 1999; Cook *et al.*, 2002), as well as their persistence (Schweiger *et al.*, 2005) and dispersal potential (Niemela, 2001; Driscoll & Weir, 2005; Barbaro & Van Halder, 2009; Brooks *et al.*, 2012).

Few studies have considered site and landscape influences on beetle community composition simultaneously (Aviron *et al.*, 2005), and those that have done this have tended to focus on agricultural landscapes (e.g. De La Peña *et al.*, 2003; Jeanneret *et al.*, 2003b; Aviron *et al.*, 2005; Dauber *et al.*, 2005; Schweiger *et al.*, 2005; Hendrickx *et al.*, 2007). Surprisingly, floodplain habitats, which have been heavily influenced by a wide range of site and landscape factors, have been substantially less well covered by assessments of relative influences of site and landscape scale factors on species composition (Baiocchi *et al.*, 2012). Yet changes beyond the limits of the floodplains themselves, need to be taken into account to provide a comprehensive picture of human-induced changes on floodplain biodiversity.

Additionally, few studies have considered detailed diversity data from two highly speciose beetle taxa, such as carabids and staphylinids, in the context of floodplain environments (e.g. Uetz *et al.*, 1979; Greenwood *et al.*, 1991; Paetzold *et al.*, 2008). Studies on carabids and spiders tend to dominate ground fauna literature due to their well-known taxonomy and ecology, and their well-established sensitivity to environmental gradients (Lövei & Sunderland, 1996; Niemelä, 1996). Despite being one of the most diverse groups within floodplain habitats (Hammond, 1998) and one of the most ecologically important insect components of the soil fauna (Bohac, 1999), the study of staphylinids has lagged well behind many other insect groups (Lott & Anderson, 2011). Staphylinid beetles are predominantly hygrophilous or mesophilous (Bohac, 1999); 422 British species are said to be associated with wetland habitats (Lott, 2003). Consequently, considering carabids and staphylinid beetles together provides increased scope for understanding these complex habitats.

This chapter therefore investigates the β-diversity of carabid and staphylinid beetles on the floodplains of three chalk rivers in Norfolk, by asking the following questions: (1) Does the composition of beetle assemblages vary significantly between the dominant habitat types of these chalk river floodplains? (2) What are the relative contributions of site-scale and landscape-scale factors in determining the composition

of beetle assemblages? (3) How can carabid and staphylinid beetle community composition inform floodplain conservation and restoration practices?

4.2 Methodology

4.2.1 Field methods

This study was conducted on three chalk rivers in Norfolk, eastern England (Figure 2.2). Five meadows, three fens and seven woodland sites were studied across the Rivers Glaven (n = 9), Bure (n = 5) and Wissey (n=1) to represent the dominant land uses of floodplain environments in these chalk rivers (Table 2.2). All floodplain sites were located in the middle reaches of the three rivers. Contemporary and historical site information has been outlined in Section 2.4.

Beetle sampling

Field research was carried out between April and September in 2009 and 2010 in order to capture both inter-annual and seasonal variations in beetle communities, and to maximise species representation. A full outline of collected samples from the 15 study sites is given in Table 3.2. Notably, Alder Carr was only sampled during the 2010 season. Data were collected using five replicate 2 x 2 m plots randomly distributed throughout each study site at a minimum distance of 10 m from each other.

Beetles were sampled using two unbaited pitfall traps per plot, situated 1m apart. The limitations of pitfall trapping are well established (Spence & Niemelä, 1994 and references therein), however this method provides a simple and effective standardized sampling method for ground dwelling arthropods, allowing for comparability across sites (Greenwood *et al.*, 1991; Apigian *et al.*, 2006). Catch sizes from pitfall traps indicate 'activity density', that is a function of both beetle movement on the soil surface and population density (Lester & Morrill, 1989) and therefore species abundance is referred to in this chapter with the understanding that these figures represent 'activity-density' (Baars, 1979; Niemalä *et al.*, 1990; Apigian *et al.*, 2006; Woodcock & Pywell, 2009). Samples from traps disturbed by small mammals, and those affected by waterlogging and overflowing, were excluded from the analysis.

Beetles were sorted and identified to species-level using keys and reference books (Joy, 1932; Tronquet, 2006; Luff, 2007; Lott, 2009; Lott & Anderson, 2011). Further explanation of identification procedures, including the consultation of reference

collections, can be found in Chapter 3. A number of similar species were grouped, as they are chiefly separable using male genitalia, which only permits the identification of male specimens. These are outlined in Section 3.2.1.

Recording of vegetation, other site parameters and landscape characteristics

Vegetation species richness was recorded within 2 x 2 m quadrats, and percentage cover estimated for each species of vascular plant present. Plants were identified to species level using identification guides by Hubbard (1984), Rose *et al.* (2006) and Jermy *et al.* (2007). Cover estimates were recorded in 5% intervals, however 1% intervals were used for cover estimates between 1 and 5%. Vegetation was sampled in May-June 2009, with further notes taken of newly appearing species throughout April-September 2009-2010 during beetle trapping.

To evaluate the effects site and landscape factors exert on beetle assemblages, a series of site and landscape descriptors were used, the collection of which is described in Section 3.2.1 and summarised in Table 3.3. This included the estimation of surrounding land use within a 250 m radius using EDINA, aerial photographs and site visits, which provided percentage-cover values for different land uses around each site. Beetles may well respond to landscape features wider than 250 m, however, short spatial distances between study sites made it necessary to restrain the focus to the immediate surrounding habitat similar to Dauber *et al.* (2005). A full table of site and landscape characteristics for the 15 floodplain sites is given in Appendix 2.

4.2.2 Statistical analysis

For each 2 x 2 m quadrat, pitfall trap capture data from 2009 and 2010 were pooled for analyses. Prior to statistical analysis, data for *Aleocharinae* species and unidentifiable female specimens were removed. A small number of species were also grouped into species aggregates due to indistinguishable morphological characteristics (see Section 3.2.1).

Beetle assemblage composition

Permutational multivariate analysis of variance (PerMANOVA) (Anderson, 2001; Barton *et al.*, 2009; Anderson *et al.*, 2011) was used to test for differences in the composition of beetle assemblages between sites, habitat types, and catchments. PerMANOVA analysis is a non-parametric multivariate version of ANOVA that tests the compositional heterogeneity that is attributed to the variation in species identities,

with p-values derived using permutations (Anderson, 2001). It compares the variability of average dissimilarity in species presence and absences within groups (here sites, habitat types and catchments) against the variability among other groups.

Staphylinid and carabid data were first transformed using Hellinger transformations due to the large number of zero-values in the datasets (Legendre & Gallagher, 2001; Axmacher *et al.*, 2009), before PerMANOVA was performed with 9999 permutations of the data. The PerMANOVA package (Anderson, 2001; Anderson, 2005) was used for analysis on individual sites as it allows for *post hoc* pairwise comparisons after PerMANOVA calculations. Due to the differences in number of sites for the different catchments and habitat types (River Bure n=5, River Glaven n=9, River Wissey n=1; woodland n=7; fen n=3; meadow n=5), single analysis calculations for between and within-habitat compositional differences could not be performed using this package. Instead, PerMANOVA with 9999 permutations was applied to the data three times with woodland and fen habitats, fen and meadow habitats and woodland and meadow habitats, and similarly with different catchments. This latter PerMANOVA analysis was carried out using the 'vegan' package in R (R Development Core Team, 2011; Oksanen *et al.*, 2012).

Permutational analysis of multivariate dispersions, also referred to as homogeneity of multivariate dispersions (HMD), was used to determine the within-site, within-habitat and within-catchment compositional heterogeneity attributed to variation in relative abundances (Anderson, 2006; Anderson *et al.*, 2006; Barton *et al.*, 2009). HMD is a multivariate analysis method that firstly calculates distances to a centroid within each pre-defined group (a measure of dispersion) and then compares this to average distances of this among different groups. A Hellinger matrix was calculated based on abundance values for both staphylinid and carabid species data separately, and calculations of distances from group centroids were calculated using ANOVA with 9999 permutations. HMD differs from PerMANOVA as it provides a measure of compositional variability in terms of average dissimilarity (or distance from the centroid), without focus on species identities. In comparison, PerMANOVA provides a measure of dissimilarity by discriminating between these species identities. Analyses were performed using the 'vegan' package in R (R Development Core Team, 2011; Oksanen *et al.*, 2012).

To visualise similarities and differences in beetle assemblage composition in different habitats, non-linear multi-dimensional scaling (NMDS) was run on chord-normalised expected species shared (CNESS) dissimilarity matrices. CNESS has been suggested to be one of the most appropriate indices for analysing β-diversity based on quantitative data as it allows the calculation of probability-based similarity using samples that can differ in sample size (parameter m) (Trueblood *et al.*, 1994). For this research, although every effort was made to ensure the return of a full dataset, not all sites were sampled at the same intensity due to inaccessibility, cattle trampling and waterlogging of some plots (see Table 3.2). Consequently, a method that allows for differing sample sizes is the most appropriate, and CNESS has been used effectively to assess carabid diversity in sites of different management intensities (e.g. Yu *et al.*, 2006; Liu *et al.*, 2010; Liu *et al.*, 2011). By varying the sample-size parameter m, the CNESS index of dissimilarity allows for analyses with different emphasis on more dominant species (smaller values of m) and on rarer species (larger values of m). Three values of m were used for the staphylinid and carabid data separately: $m = 1$ for both; the largest common sample size for carabids ($m = 3$) and staphylinids ($m = 9$); and the largest sample size ensuring that three samples from each habitat type were included in the analysis for carabids ($m = 7$) and staphylinids ($m = 17$). NMDS is an iterative search for the ranking and placement of samples along ordination axes that tries to minimise the 'stress' of those configurations, where stress represents the degree to which data in the original space (dissimilarity matrix) is dissimilar to the distance in ordination space (McCune *et al.*, 2002). Stress levels under 0.2 are seen as a suitable fit and hence represent fairly accurate depictions in the respective ordination plots, in comparison to higher values (Clarke, 1993). The CNESS dissimilarity matrix was calculated using COMPAH (Gallagher, 1998) and the NMDS was performed using the 'MASS' and 'vegan' packages in R (Venables & Ripley, 2002; R Development Core Team, 2011; Oksanen *et al.*, 2012).

Influence of site and landscape factors on beetle assemblages

To analyse the influence of habitat and landscape factors on the floodplain beetle communities, Redundancy Analysis (RDA) was performed on carabid and staphylinid abundance data, separately. This analysis aims to capture the variation in community data that can be explained by specific and measured environmental variables (Lepš & Šmilauer, 2003). The ordination method visually arranges plots in a multidimensional graphical space, constraining species and samples by the environmental variables included in the analysis.

Environmental variables used in this analysis are given in Table 3.3. Categorical variables, such as habitat type, were coded using dummy variables to allow for their inclusion in analysis. Normal distributions were checked using QQ-plots and Shapiro-Wilk Normality Tests for both plot data and site data, and data were transformed where necessary. A Principal Components Analysis (PCA) was performed on arc-sine transformed vegetation species data and a broken stick graph used to identify the most important principal components (PCs) to be included as variables in the environmental data matrix. Carabid and staphylinid data were both transformed using Hellinger transformations. An inclusive forward selection procedure, using Akaike's Information Criterion (AIC) to find the optimal model, was performed on the environmental data, to identify factors best explaining the variance in staphylinid and carabid assemblages. AIC is based on goodness of fit (high constrained inertia), but values are corrected for the number of included explanatory parameters (Bozdogan, 1987; Oksanen, 2011). Collinearity was also analysed to ensure that the most suitable variables were chosen for each model and the significance of each explanatory variable was tested using ANOVA with 9999 permutations.

In addition to RDAs, variance partitioning analysis (pRDA) was conducted on carabid and staphylinid abundance data to analyse the relative importance of site, landscape and spatial factors in structuring the beetle assemblages. This approach partitions the total percentage of variation explained by an RDA into unique and common contributions for distinct sets of specified predictors (Borcard *et al.*, 1992). Significant models identified for site and landscape factors in the RDA were used for the site and landscape contributions within the pRDA. Spatial predictors were constructed using XY coordinates of each plot. Using a Euclidean distance matrix of these coordinates, principal coordinate analysis (PCoA) was performed and the positive eigenvalues of the PCoA were used as a set of spatial predictors for the third variable in the pRDA. PCoA allows for the ordination of data with a specified distance matrix, and therefore preserves the Euclidean distances of this data (Anderson & Willis, 2003). Species with less than five specimens in all collections were removed prior to analysis to prevent overdue influence of rare species on the pRDA. Carabid and staphylinid species abundance data were again Hellinger transformed prior to analysis (Legendre & Gallagher, 2001), which is a well-suited transformation for the variation partitioning based on RDA (Borcard & Legendre, 2002; Peres-Neto *et al.*, 2006). The significance of each fraction was tested using 9999 permutations. Both RDA and pRDA analyses were

carried out using the 'ape' and 'vegan' packages in R (De Cáceres & Legendre, 2009; R Development Core Team, 2011).

As emphasised by Anderson and Cribble (1998) and Jeanneret *et al.* (2003b), causal effects from variance partitioning require an appropriate experimental design and analysis before full conclusions can be drawn. An experimental setting was clearly outside the scope of this study, and causal analysis was therefore not feasible. However, to reduce the inclusion of redundant variables and subsequent increased explanation of variance due to chance alone, forward selection procedures and further variable selection scrutiny was implemented.

Links between beetle assemblages, vegetation composition and the spatial distribution of plots

Mantel tests were carried out to establish the similarity between the species turnover patterns in beetle assemblages, vegetation composition and the spatial distribution of plots and sites. Mantel tests evaluate the correlation between two independent distance matrices that describe the relationships among an identical set of sampling plots (Legendre & Fortin, 1989), in this case between the CNESS dissimilarity matrices (m=1) for carabid and staphylinid data, Bray-Curtis dissimilarity matrix of the vegetation composition data, and a Euclidean dissimilarity matrix of the spatial coordinates of plots. The significance of each Mantel calculation was tested using 9999 permutations and performed using the 'vegan' package in R (R Development Core Team, 2011; Oksanen *et al.*, 2012). As this method uses resemblance matrices (dissimilarity matrices) rather than the original data, it has been subject to criticism (Dutilleul *et al.*, 2000; Peres-Neto & Jackson, 2001; Legendre & Fortin, 2010; Gioria *et al.*, 2011). However, the Mantel test remains a widely used statistical technique to compare the association between two data matrices, as it is robust, flexible and simple (Gioria *et al.*, 2011).

Table 4.1 Summary of analytical methods used in Chapter 4

Analytical Method	Application
Permutational multivariate analysis of variance with post-hoc pairwise comparisons (PerMANOVA)	To assess the differences in assemblage composition between sites, habitats and catchments using relative species abundances.
Permutational analysis of multivariate dispersions (HMD)	To assess the differences in heterogeneity of beetle assemblages between sites, habitats and catchments using relative abundances but with no consideration to species identities.
Non-metric multidimensional scaling (NMDS)	To visualise similarities and differences in beetle assemblage composition across all plots, habitats and catchments.
Redundancy analysis (RDA)	To assess the influence of site and landscape factors on beetle assemblage composition.
Variance partitioning (pRDA)	To establish the relative influence of site, landscape and spatial factors on beetle assemblage composition.
Mantel tests	To determine correlations between beetle assemblages, vegetation composition and spatial distribution of plots and sites.

4.3 Results

A total of 8727 carabid and staphylinid beetles were collected in 2009 and 2010. Of these, 8060 were positively assigned to one of 142 species. Members of the staphylinid subfamily *Aleocharinae* (611 specimens) were not identified to species level and excluded from analyses. Species abundances grouped by habitat are given in Section 3.3.

Beetle community characteristics

Catchments differed in carabid and staphylinid assemblages, as revealed by PerMANOVA analysis (Table 4.2). Specifically, meadow and woodland habitats differed in carabid assemblages (meadow: $F=5.83$, $p<0.01$; woodland: $F=3.33$, $p<0.01$, respectively), however *post hoc* analysis suggested no significant difference in carabid assemblage composition between the River Bure and River Wissey woodlands. Significant differences between catchments were identified for woodland staphylinid assemblages ($F=3.92$, $p<0.01$), but not between meadow habitats ($F=1.09$, $p=0.32$).

A general comparison between habitat types revealed that staphylinid and carabid assemblage composition was significantly different between habitats (staphylinid

F=6.68, p<0.01; carabid F=4.54, p<0.01; Table 4.2), and *post hoc* analysis confirmed that this was true for both carabid and staphylinid beetles for comparisons between each of the three habitat types (Table 4.3). Assemblage composition significantly differed between sites for both carabid and staphylinid beetles (F=4.96, p<0.01; F=5.50, p<0.01, respectively). *Post hoc* comparisons are summarised for carabid and staphylinid beetles in Appendix 5.

Heterogeneity in assemblages also varied between catchments, as shown by permutational multivariate dispersion (HMD) comparisons for both carabid and staphylinid assemblages (F=5.970, p<0.01 and F=4.667, p<0.01, respectively; Table 4.4). The River Glaven showed the highest distance to centroid for carabids (HMD=0.558), and the River Bure for staphylinids (HMD=0.462), suggesting these rivers support more heterogeneous carabid and staphylinid assemblages, respectively. HMD did not vary significantly between habitat types for carabid or staphylinid beetles (F=0.180, p=0.84 and F=2.480, p=0.10, respectively), yet was significantly different between sites for staphylinid beetles (F=2.078, p=0.03). Mean distance from centroid was lowest for Glaven Farm, a fen habitat on the R. Glaven and highest for Moorgate Meadow, a meadow on the R. Bure (HMD=0.150 and 0.406 respectively). In comparison, HMD did not vary significantly between sites for carabid beetles (F=1.197, p=0.30). Lowest values were found in RPC and highest values in AC (HMD=0.250 and 0.525 respectively). Additionally, the results suggest that carabid communities are more heterogeneous than staphylinid assemblages as eleven out of fifteen sites, all habitats and catchments showed higher HMD values for carabids than for staphylinids (marked with a † in Table 4.4).

Table 4.2 PerMANOVA calculations between sites, habitats and catchment. For pairwise comparisons, terms were considered significantly different if p < 0.01.

Factor	Beetle	df	Mean SS	F Model	R^2	P-value	Post Hoc comparisons
River (Bure and Glaven all sites)	Carabid	1	2.06	6.42	0.09	<0.01	Glaven and Bure sites significantly different.
	Staphylinid	1	1.08	5.13	0.07	<0.01	Glaven and Bure sites significantly different.
River (meadow sites only)	Carabid	1	1.46	5.83	0.20	<0.01	Glaven and Bure meadow sites significantly different
	Staphylinid	1	0.23	1.09	0.05	0.32	Glaven and Bure meadow sites *not* significantly different.
River (woodland sites only including AC from Wissey)	Carabid	2	0.94	3.33	0.17	<0.01	Glaven and Bure woodland sites significantly different; Glaven and Wissey woodland sites significantly different; Bure and Wissey woodland sites *not* significantly different.
	Staphylinid	2	0.68	3.92	0.20	<0.01	Glaven and Bure woodland sites significantly different; Glaven and Wissey woodland sites significantly different; Bure and Wissey woodland sites significantly different.
Habitat	Carabid	2	1.15	4.54	0.11	<0.01	See Table 4.3.
	Staphylinid	2	1.33	6.68	0.16	<0.01	See Table 4.3.
Site	Carabid	14	0.97	4.96	0.54	<0.01	See Appendix 5.
	Staphylinid	14	0.68	5.50	0.56	<0.01	See Appendix 5.

*Table 4.3 PerMANOVA calculations between habitat types. F-statistics are displaced. The larger values of F reflect higher compositional differences between groups. All groups were significantly different; significance is shown as ** <0.01.*

		Fen	Woodland
Carabid	Meadow	4.19**	5.74**
	Fen		3.40**
Staphylinid	Meadow	5.98**	5.23**
	Fen		9.16**

Table 4.4 Permutational analysis of multivariate dispersions (HMD) within catchments, habitats and sites. Values represent mean distances to centroid ± variance. † highlights the higher value in a comparison between carabid and staphylinid results for each category

Category	Site	Staphylinid	Carabid
CATCHMENT			
Glaven	All	0.422 ± 0.013	†0.558 ± 0.008
Bure	All	0.462 ± 0.022	†0.476 ± 0.008
Wissey	All	0.272 ± 0.020	†0.525 ± 0.022
ANOVA between catchments		**F=4.667 p=0.01**	**F=5.970 p<0.01**
HABITAT			
Meadow	All	0.444 ± 0.012	†0.532 ± 0.006
Fen	All	0.353 ± 0.040	†0.475 ± 0.011
Woodland	All	0.431 ± 0.012	†0.531± 0.017
ANOVA between habitats		**F=2.480 p=0.10**	**F=1.565 p=0.22**
SITE			
Meadow	HCA	0.295 ± 0.021	†0.400 ± 0.007
	HR	0.224 ± 0.004	†0.459 ± 0.016
	HM	0.375 ± 0.004	†0.377 ± 0.029
	MM	†0.406 ± 0.001	0.344 ± 0.014
	IB	0.250 ± 0.004	†0.375 ± 0.022
Fen	HLF	0.285 ± 0.010	†0.368 ± 0.027
	GF	0.150 ± 0.003	†0.314 ± 0.015
	WF	0.210 ± 0.006	†0.328 ± 0.003
Woodland	HLW	†0.370 ± 0.025	0.297 ± 0.043
	HW	0.284 ± 0.006	†0.451 ± 0.024
	WW	0.299 ± 0.003	†0.387 ± 0.043
	MC	0.298 ± 0.013	†0.400 ± 0.008
	SC	†0.356 ± 0.007	0.327 ± 0.016
	RPC	†0.352 ± 0.007	0.250 ± 0.014
	AC	0.272 ± 0.020	†0.525 ± 0.023
ANOVA between sites		**F=2.078 p=0.03**	**F=1.197 p=0.30**

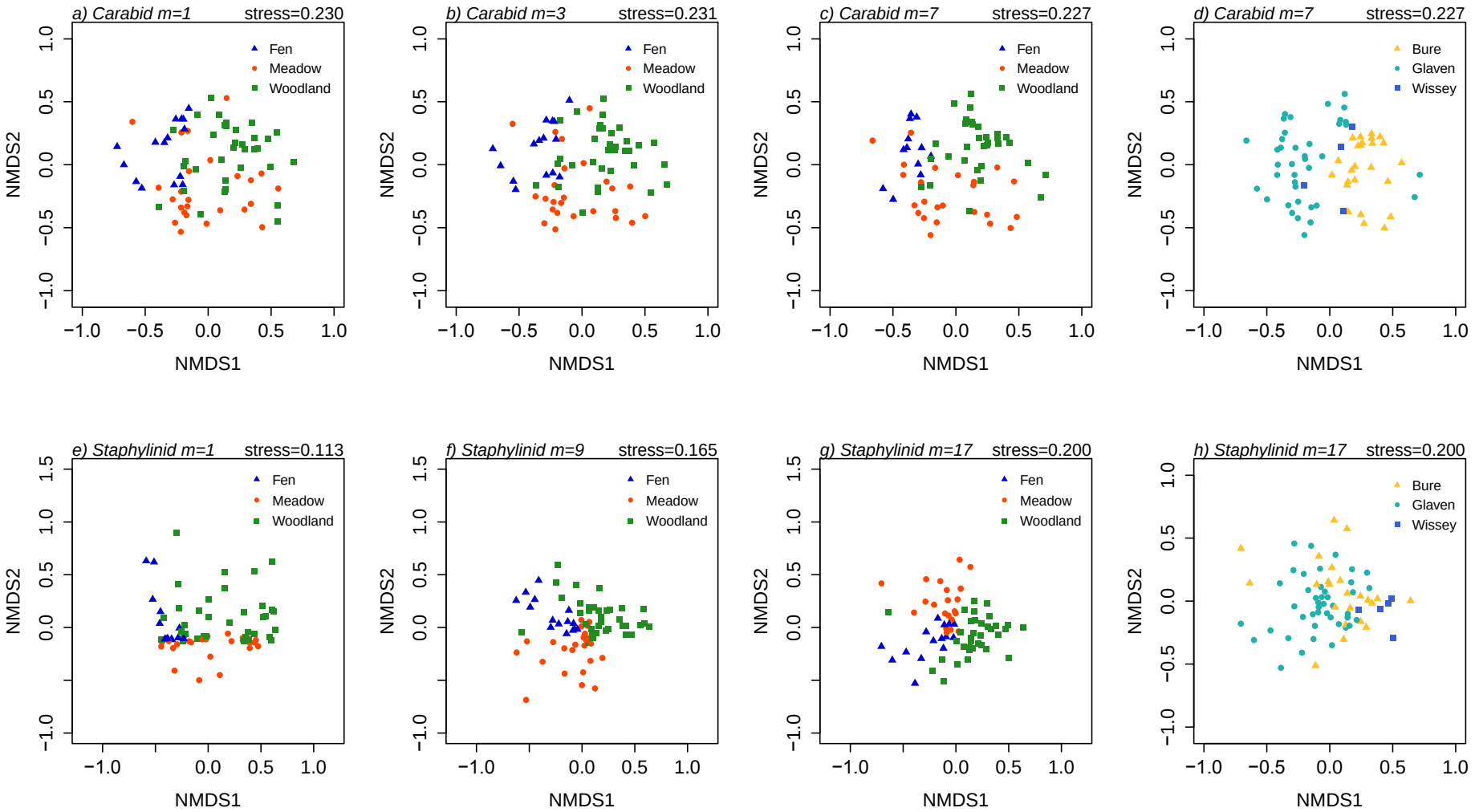


Figure 4.1 CNESS-based non-metric multidimensional scaling (NMDS) of carabid (a-d) and staphylinid (e-h) beetle assemblages with varying sample size parameter m. *Ordinations a-c and e-g are coloured according to habitat type. Ordinations d and h are coloured by river. Three values of m (sample size) were used for the staphylinid and carabid data separately: m=1 for both; the largest common sample size for carabids (m=3) and staphylinids (m=9); and the largest sample size ensuring that three samples from each habitat type were included in the analysis for carabids (m=7) and staphylinids (m=17).*

Community structure

Stress levels were below 0.2 for all values of *m* in the 2-dimensional staphylinid NMDS diagrams (Figure 4.1.e-h) suggesting a realistic visualisation of dissimilarity in the NMDS in comparison to the calculated CNESS dissimilarity matrix. However, carabid plot stress levels were 0.230, 0.231 and 0.237 for *m*=1, *m*=3 and *m*=7, respectively, rendering their interpretation slightly more problematic (Figure 4.1.a-d). With an emphasis on dominant carabid species (*m*=1) and rarer species (*m*=7), no clear distinction can be made between meadow, fen and woodland habitats (Figure 4.1.a-c). In comparison, staphylinid assemblages showed a clear distinction between different habitats for all values of *m* (Figure 4.1.e-g). However, there was still a degree of overlap in staphylinid assemblages between the different habitats, suggesting similarities particularly in terms of dominant species. This is shown by the clustering of different habitat plots around the centre of each ordination diagram.

There was a clear distinction between the carabid assemblages of the River Bure and Glaven catchments, while the assemblages of the River Wissey site were not distinct (overlapping with other plots and located in the centre of the diagram, Figure 4.1.d). This was corroborated by the PerMANOVA results, which also recorded no significant differences between the River Bure and Wissey woodland assemblages (Table 4.2). No clear distinctions in staphylinid assemblages were evident between river catchments (Figure 4.1.h); this was also reflected in the PerMANOVA results, which revealed no significant differences between River Bure and Glaven meadow habitats (Table 4.2). However the River Wissey showed more distinct staphylinid assemblages, displayed in the ordination as a distinct cluster of plots (Figure 4.1.h).

Influence of site and landscape variables on beetle assemblages

RDA analysis revealed some significant site and landscape influences on carabid and staphylinid assemblages (Table 4.5 and Figures 4.2-4.5). For carabid species, at a site scale, significant influences were habitat type, area, grazing and cutting (model AIC=-49.09, F=5.51, $p<0.01$; Table 4.5). Assemblages showed differences between habitats, although some overlapping of a few plots in the ordination suggests there were some similarities in specific assemblages (Figure 4.2.a). Area differentiated fens from other habitats, as can be seen by the position of fen sites GF, WF and HLF on the area gradient (Figure 4.2.a). Similarly cutting and grazing management differentiated meadow plots from woodland plots. A number of species showed a clear preference for individual habitats and their associated sets of environmental parameters (Figure 4.2.b): *Nebria brevicollis* and *Patrobus atrorufus* showed a strong

preference for woodland habitats, *Amara communis*, *Bembidion mannerheimii*, *Pterostichus strenuus* and *Pterostichus niger* for meadow habitats, and *Agonum emarginatum, Agonum fuliginosum and Pterosticus minor* for fen habitats. An additional notable association is that of *Carabus granulatus* (one of the largest carabid species) with large sites, while *Pterostichus nigrita* agg., (a medium sized carabid species) showed highest abundance at smaller sites.

In addition to site-scale influences, edge density (ED), landscape pattern (D_1), and surrounding meadow (SM) also significantly influenced carabid community composition, as identified by forward selection methods (model AIC=-45.86, F=6.40, $p<0.01$; Table 4.5). There was some distinction in assemblage composition between habitats (Figure 4.3.a). Woodland assemblages were associated with simple surrounding landscapes dominated by meadows. In comparison, high edge densities differentiated fen assemblages, and complex surrounding landscape differentiated meadow assemblages. Predominantly, meadow sites seem to be surrounded by other habitats rather than by further meadows, highlighting the mosaic structure of different land use and habitat types along these river reaches. Again, a number of species showed a high affiliation with individual habitats, but potentially more so with different landscape elements (Figure 4.3.b). The abundances of *Pterostichus niger*, *Pterostichus diligens* and *Anisodactylus binotatus* seem to be strongly influenced by a complex surrounding landscape, whereas *Nebria brevicollis, Patrobus atrorufus, Pterostichus madidus* and *Loricera pilicornis* showed more association with simple landscapes. *Carabus nemoralis* was associated with high edge densities and may therefore be associated with respective fine floodplain landscape mosaics. All of these species are abundant across the British Isles and are generalists, often with preference for wetland habitats (Luff, 2007). Contrastingly, a number of species in the centre of the ordination are specialists: *Bembidion mannerheimii* is known to specialise on damp grasslands and shaded habitats, *Agonum piceum* is a rare fen specialist, *Agonum emarginatum* a wetland specialist and *Acupalpus dubious* is a specialist to litter and tussocky habitats near freshwater (Lott, 2003; Luff, 2007).

*Table 4.5 Significant site and landscape variables for RDAs on carabid and staphylinid assemblages. Significance is shown as ** <0.01.*

		Site variables	**Landscape variables**
Carabidae		Habitat**	Edge density**
		Area**	D_1 – Landscape pattern**
		Grazing**	Surrounding meadow**
		Cutting**	
	Model	**AIC=-50.95, F=5.991, p<0.01**	**AIC=-45.86, F=6.40, p<0.01**
Staphylinidae		Habitat**	Edge density**
		Grazing**	D_1 – Landscape pattern**
		Area**	Surrounding arable**
	Model	**AIC=-91.62 F=8.84, p<0.01**	**AIC=-80.09, F=6.08, p<0.01**

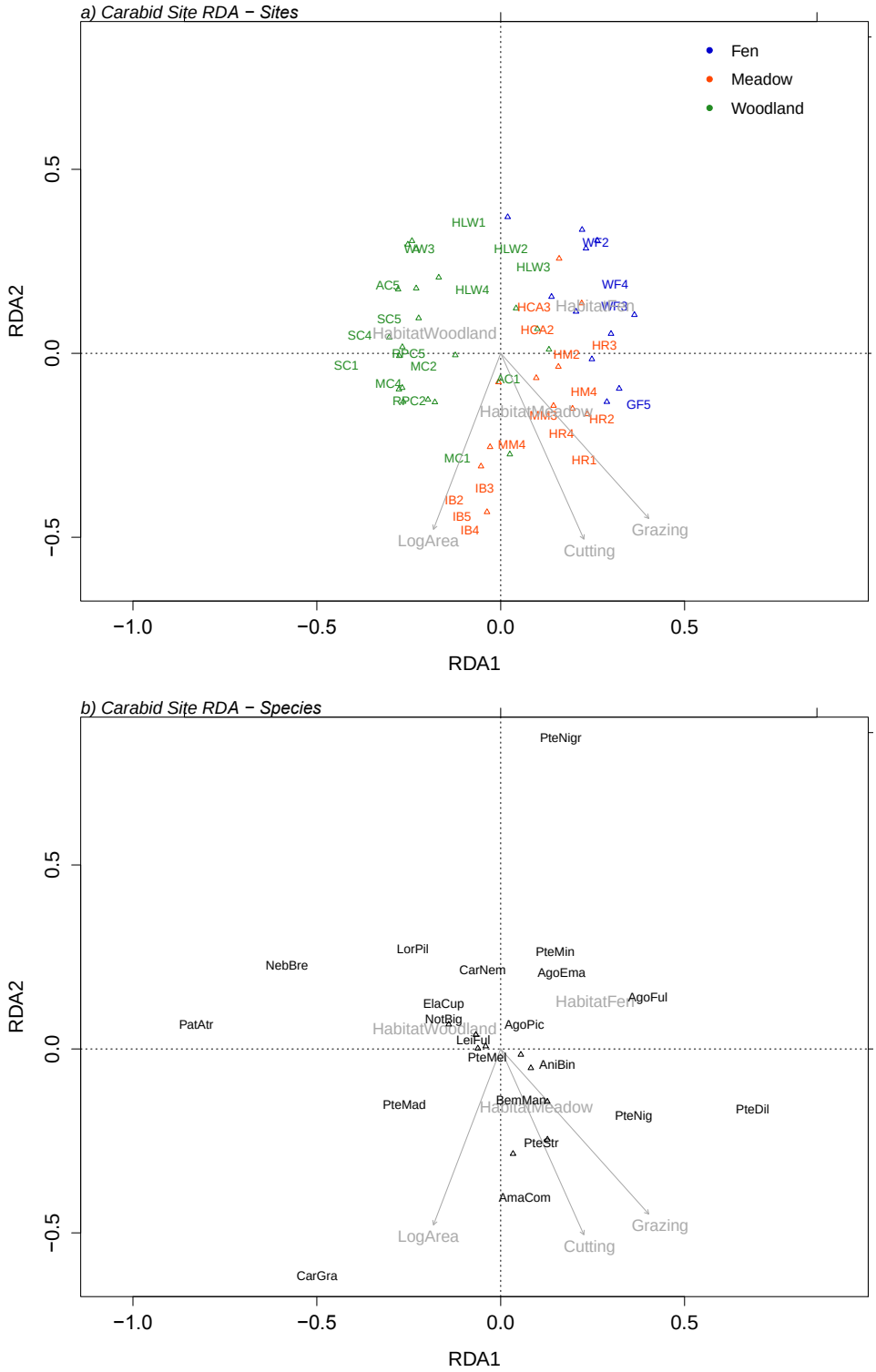


Figure 4.2 Ordination (RDA) of carabid assemblages in relation to site variables. Plots are labelled according to their site name and colours represent the different habitat types. Arrows represent significant site variables (LogArea - site area, grazing and cutting). Habitat labels (HabitatFen, HabitatMeadow and HabitatWoodland) represent the centroids of the factor variable habitat. Species are abbreviated (see Appendix 6 for a full list of species' abbreviations). Labelling priority is given to those species or samples that are most abundant or most diverse, respectively, using the inverse of Simpson's diversity index. Those species not labelled are marked as an open triangle.

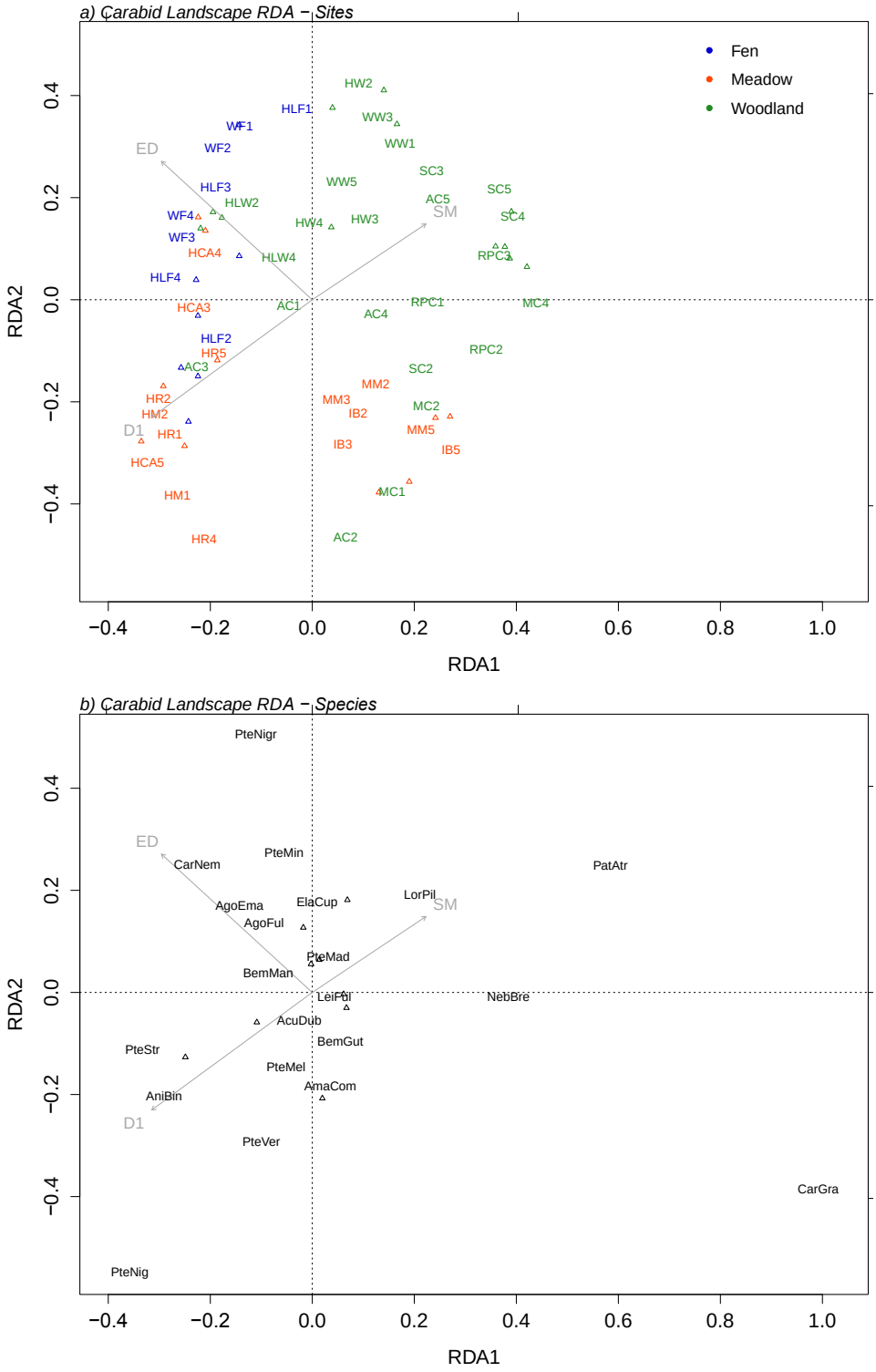


Figure 4.3 Ordination (RDA) of carabid assemblages in relation to landscape variables. Plots are labelled according to their site name and colours represent the different habitat types. Arrows represent significant landscape variables (landscape pattern - D_1, edge density - ED and percentage of surrounding meadow - SM). Species are abbreviated (see Appendix 6 for a full list of species' abbreviations). Labelling priority is given to those species or samples that are most abundant or most diverse, respectively, using the inverse of Simpson's diversity index. Those species not labelled are marked as an open triangle.

For staphylinid assemblages, habitat, grazing and site area were strong determinants of species variation (model AIC=-91.62 F=8.84, p=<0.01; Table 4.5). Similar to carabid assemblages, area differentiated fens from other habitats, and grazing largely separated meadow and woodland communities (Figure 4.4.a). Staphylinid assemblages of HLF displayed a distinct community composition and were particularly associated with *Staphylinus erythropterus*, which was found in abundance at this site. The species has been correspondingly associated with open habitats on poor soils such as fens (Lott & Anderson, 2011). *Philonthus decorus* showed strong preference to woodland habitats as well as *Lathrobium brunnipes* and *Anotylus sculpturatus* agg, which are all generalists but the first two are associated with shaded habitats. *Philonthus cognatus, Quedius molochinus* and *Tachinus marginellus* - all generalists - were characteristic of meadow habitats. *Rugilus erichsonii* was also characteristic of this habitat type and in particular high grazing intensity, however this species is a very hygrophilous, fen specialist, and is frequently found in small-scale springs and flushes within meadows (Lott & Anderson, 2011). Despite specific species associations, there was a dominance of species common to all habitat types, shown by clustering of species around the centre of the ordination (Figure 4.4.b).

At a landscape scale, edge density (ED), landscape pattern (D_1) and surrounding arable land (SA) significantly influenced staphylinid assemblage composition (model AIC=-80.09, F=6.08, p<0.01; Table 4.5). The ordination of the staphylinid landscape factors (Figure 4.5.a) shows that edge density is correlated with the first axis, and landscape pattern and surrounding arable were correlated with the second axis. A distinct pattern between habitat types is evident: meadow staphylinid assemblages were influenced by the high surrounding land use dominance, and fen habitats by high edge densities. Again, a dominance of species common to all habitat types is evident by the clustering of species around the centre of the ordination (Figure 4.5.b), however landscape variables demonstrated a strong influence on a number of staphylinid species. The species *Anotylus rugosus* was associated with high edge densities whereas *Tachinus rufipes* was associated with habitats of low edge density, and therefore could be related to less disturbed sites. Both are generalist species associated with damp habitats (Lott, 2009; Lott, 2011). *Rugilus erichsonii* was linked to more simplistic surrounding land use, whereas *Proteinus brachypterus*, *Stenus bimaculatus* and *Philonthus decorus* and *Staphylinus erythropterus* were influenced by higher surrounding landscape complexity. *Gabrius breviventer* and *Tachyporus dispar*, which are both generalists, were associated with surrounding arable lands.

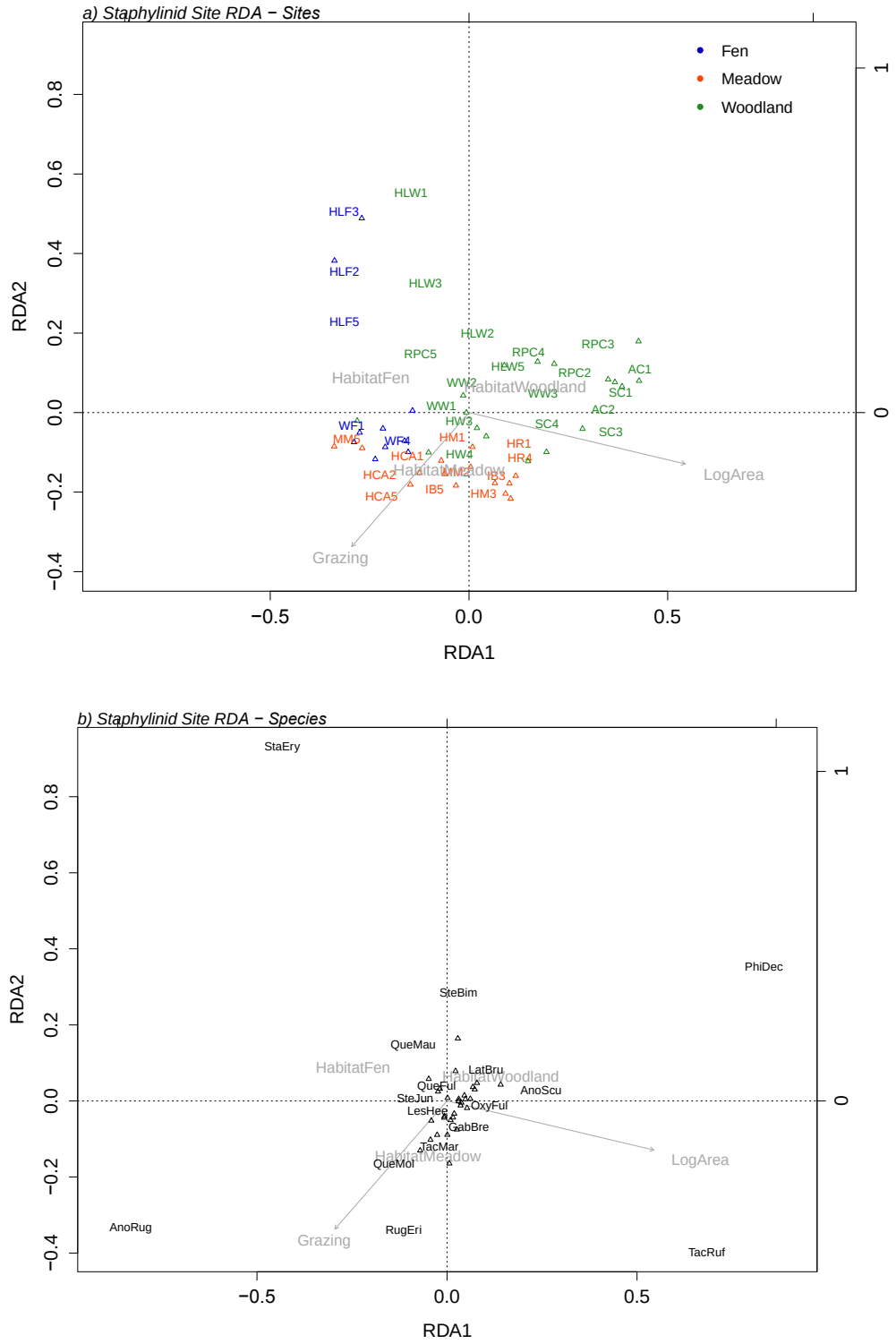


Figure 4.4 Ordination (RDA) of staphylinid assemblages in relation to site variables. Plots are labelled according to their site name and colours represent the different habitat types. Arrows represent significant site variables (grazing and site area - LogArea). Habitat labels (HabitatFen, HabitatMeadow and HabitatWoodland) represent the centroids of the factor variable habitat. Species are abbreviated (see Appendix 6 for a full list of species' abbreviations). Labelling priority is given to those species or samples that are most abundant or most diverse, respectively, using the inverse of Simpson's diversity index. Those species not labelled are marked as an open triangle.

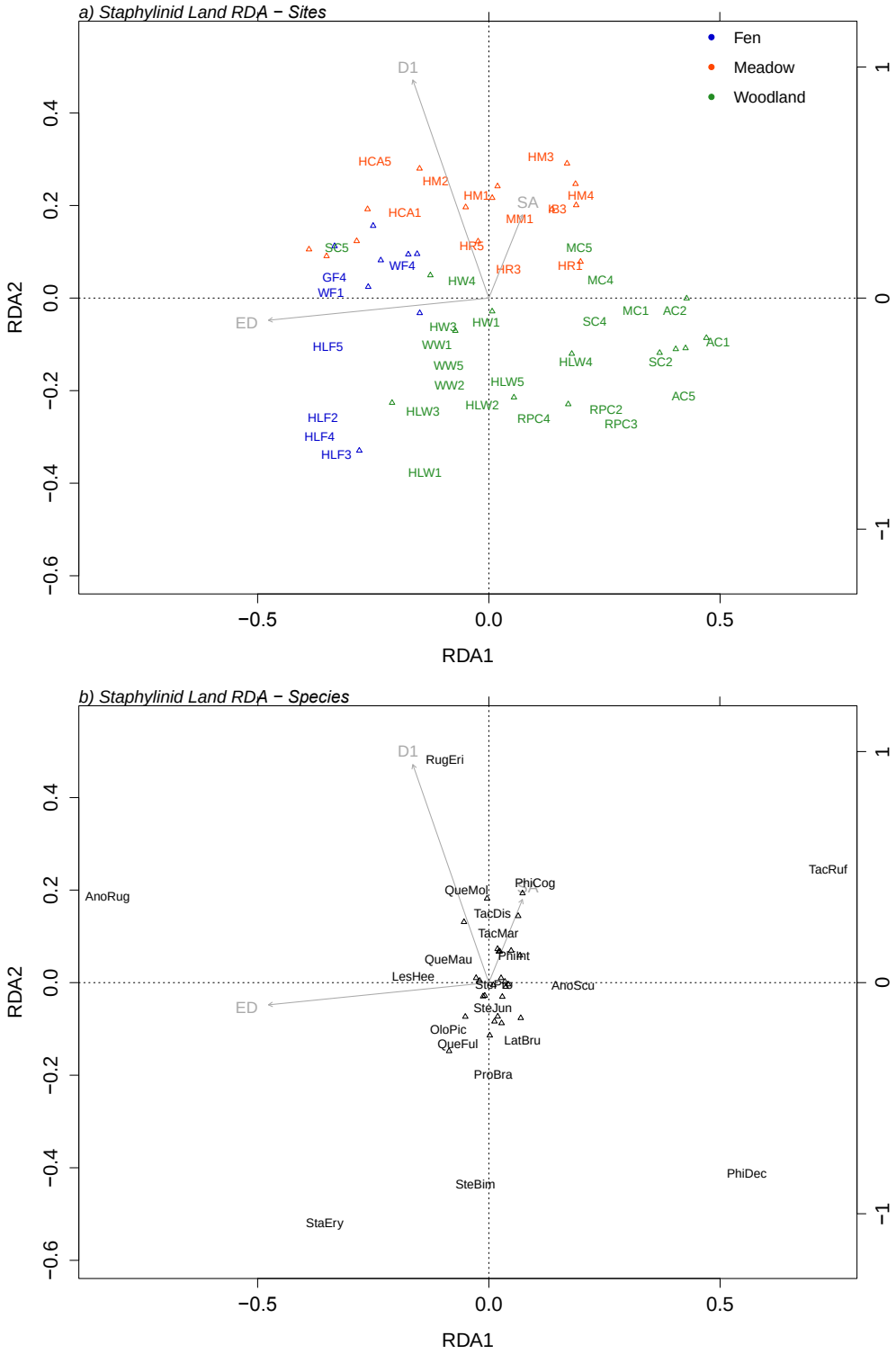


Figure 4.5 Ordination (RDA) of staphylinid assemblages in relation to landscape variables. Plots are labelled according to their site name and colours represent the different habitat types. Arrows represent significant landscape variables (edge density – ED, landscape pattern – D_1 and surrounding arable land – SA). Habitat labels (HabitatFen, HabitatMeadow and HabitatWoodland) represent the centroids of the factor variable habitat. Species are abbreviated (see Appendix 6 for a full list of species' abbreviations). Labelling priority is given to those species or samples that are most abundant or most diverse, respectively, using the inverse of Simpson's diversity index. Those species not labelled are marked as an open triangle.

A clear dominant influence of site variables on carabid and staphylinid assemblages was evident from the variance partitioning analysis (Figure 4.6 and 4.7, respectively). The total variability in carabid assemblage composition explained by the set of site, landscape and spatial variables was 34.6%. Site-specific characteristics alone [S|L+SP] explained 16.0% and landscape-specific factors alone [L|S+SP] explained 3.6%. The combined fraction of site and landscape factors [S+L] explained the majority of explainable variance, 30.9%. The total variability in staphylinid assemblages explained by all variables was 40.1%, of which site-specific characteristics alone [S|L+SP] explained 16.6% and landscape-specific factors alone [L|S+SP] explained 8.7%. Similarly to carabid assemblages, the combined fraction of site and landscape factors [S+L] explained the majority of explainable variance at 33.9%. The location of plots spatially [SP|S+L] explains a small but significant part of the variation for carabid beetles (3.3%), but a larger amount of variation for staphylinid beetles (6.5%). For staphylinids, total variance explained by the spatial distribution of plots, without conditioning for habitat and landscape factors [SP], is 13.7%.

These results indicate the dominance of site factors in influencing the composition of carabid and staphylinid assemblages, although it must be noted that the specific site factors considered in the analysis differ between beetle families. They also highlight the interacting nature of site, landscape and spatial factors, particularly for staphylinid beetles for which the joint contribution of site, landscape and spatial factors was 11.7%.

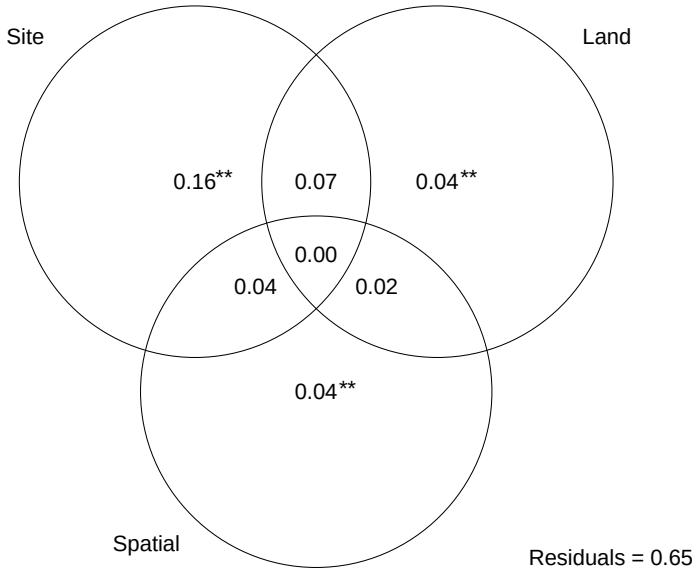


*Figure 4.6 Variance partitioning of the relative influence of site factors, landscape factors and spatial location on carabid assemblage composition. Values represent the proportion of the adjusted variation (total = 1), which have been rounded to 2 decimal places. Significance for each calculation is shown as '**' <0.01.*

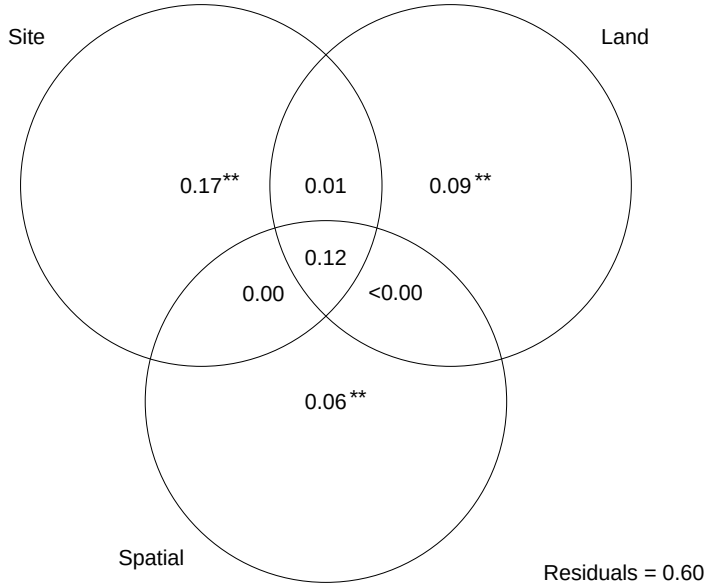


*Figure 4.7 Variance partitioning of the relative influence of site factors, landscape factors and spatial location on staphylinid assemblage composition. Values represent the proportion of the adjusted variation (total = 1), which have been rounded to 2 decimal places. Significance for each calculation is shown as '**' <0.01.*

Similarity between beetle communities, vegetation and the spatial setting

Mantel and partial Mantel tests were performed to assess the similarity between carabid and staphylinid communities, vegetation communities and the spatial distribution of sites throughout the landscape (Table 4.6). The first plot from Alder Carr (River Wissey) was removed from this analysis as no carabid beetles were recorded from that sample and Mantel tests require identical sample sets.

The results indicated no significant similarity between the carabid and staphylinid assemblages (R=0.018, p=0.29). Carabid assemblages were significantly correlated with changes in the vegetation composition (R=0.213, p<0.01). Correlations between changes in staphylinid communities and vegetation composition were also significant (R=0.245, p<0.01). Staphylinid communities were significantly linked to the spatial setting of the study (R=0.233, <0.01), while no significant links were found between spatial distribution and carabid community composition, which was visually displayed in the NMDS diagrams (Figure 4.1). A further test between spatial and vegetation matrices similarly recorded a significant correlation between these two (R=0.184, p<0.01).

Table 4.6 Mantel and partial Mantel results between carabid and staphylinid communities (CNESS dissimilarity matrix), vegetation communities (Bray-Curtis dissimilarity matrix) and the spatial dataset (Euclidean dissimilarity matrix). R represents the correlation between the dataset using the Pearson statistic.

Mantel Test	**R**	**p**
Carabidae and Staphylinidae	0.018	0.29
Carabidae and vegetation	**0.213**	**<0.01**
Staphylinidae and vegetation	**0.245**	**<0.01**
Carabidae and spatial	0.058	0.13
Staphylinidae and spatial	**0.233**	**<0.01**
Vegetation and spatial	**0.184**	**<0.01**
Partial Mantel		
Carabidae and Staphylinidae excluding any spatial component	0.004	0.43
Carabidae and Staphylinidae excluding any vegetation component	-0.036	0.85
Carabidae and vegetation, excluding any spatial component	**0.206**	**<0.01**
Staphylinidae and vegetation excluding any spatial component	**0.211**	**0.03**

4.4 Discussion

4.4.1 Beetle communities on floodplains

Examining the beetle β-diversity within chalk floodplains allows for a comprehensive understanding of the influences of site- and landscape-scale factors on beetle assemblages within these environments. It supplements the interpretation of α-diversity patterns, which condense biotic information into a single value, thereby reducing the interpretability due to information loss (Jeanneret *et al.*, 2003a), and potentially limiting the use of data for informing management practices and habitat conservation.

Habitat type should play an important part in determining beetle species composition because it represents a sum of all abiotic factors characterising a site (Jeanneret *et al.*, 2003b), and accordingly, significant differences in beetle community composition were found between chalk floodplain habitat types in this study. Communities differing in species composition are often associated with different habitats as they are adapted to take advantage of the ecological niches and environmental characteristics within (e.g. Luff *et al.*, 1989; Rosenzweig, 1995; Liu *et al.*, 2010). However, a notable result from this study was that whilst assemblages varied significantly between habitat types in terms of species composition, the general level of heterogeneity within these communities (as measured by HMD analysis) was similar across sites and habitat types. This suggests that floodplain environments provide habitats for different but equally heterogeneous beetle communities.

Surprisingly, within-site carabid communities were found to be more heterogeneous than staphylinid assemblages, shown by predominantly higher site, habitat and landscape HMD values. Many staphylinid samples were dominated by a number of common species. Notably, *Anotylus rugosus* and *Tachinus rufipes* were each represented by over 1500 individuals across all sites (Figure 4.8). This dominance may have influenced levels of relative abundance heterogeneity. As HMD is a rather new analytical technique (Anderson, 2006; Anderson *et al.*, 2006) there are few applications in the literature for carabid beetles (e.g. Barton *et al.*, 2009; Barton *et al.*, 2010; Gibb & Cunningham, 2010), and to the author's knowledge none for staphylinid beetles. The analysis method is also largely used to compare sites as opposed to the heterogeneity of a single site. As such, no direct comparisons of site, habitat and catchment values can be drawn with other studies.

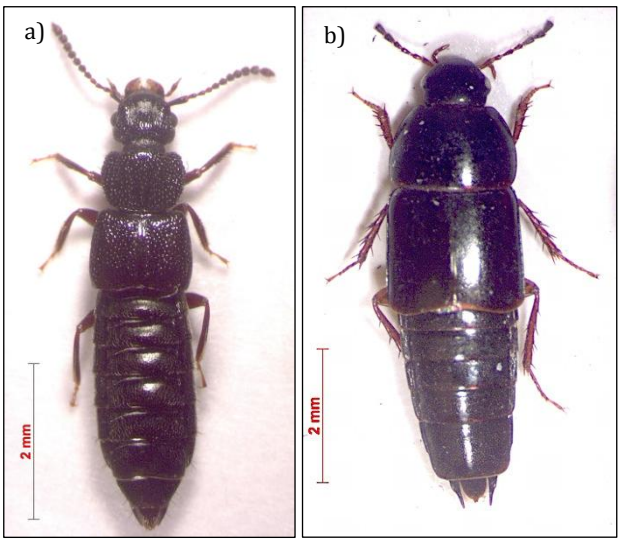


Figure 4.8 Dominant staphylinid specimens a) Anotylus rugosus and b) Tachinus rufipes

The dominance of a number of species common to all habitats may be linked to the fragmented state of the floodplain landscapes. With increasing anthropogenic influence and fragmentation of habitats, the abundances of generalist insect species commonly increases, while specialist species strongly decrease (Jonsen & Fahrig, 1997; Kotze & O'Hara, 2003). This pattern relates to the ability of species to tolerate anthropogenic disturbances, favouring generalists that utilise the increasing variety of resources available to them (Jonsen & Fahrig, 1997). Specialisation is often associated with traits that enable species to occupy specific niches, which on the negative side can leave these specialist species more vulnerable to extinction (McKinney, 1997). For example, larger species with reduced wing development, have shown vulnerability to habitat fragmentation due to their limited ability to disperse between habitat fragments (Brooks *et al.*, 2012). Additionally, research has shown that specialist carabid beetles are predominantly present in old, large habitat patches (Assmann, 1999; Niemela, 2001; Kotze & O'Hara, 2003), which have disappeared from many of the floodplains of western Europe (Petts, 1998). Consequently, increasing habitat fragmentation in floodplain environments has reduced abundances and often led to the extinction of specialist beetles, which might explain the dominance of generalists observed in this study.

4.4.2 Influence of site and surrounding landscape characteristics on beetle β-diversity

Site variables

Strong associations have been drawn between beetle communities and management practices at a site-scale (e.g. Jeanneret *et al.*, 2003b; Aviron *et al.*, 2005; Liu *et al.*, 2010), which are confirmed by the results of this study. Habitat type, vegetation management and area fraction alone explained a significant portion of variation in species composition for both families.

Cutting and grazing form the main management practices used to maintain and improve the quality of calcareous grasslands (Woodcock *et al.*, 2005a) and fen habitats (McBride *et al.*, 2011). Cutting vegetation within these habitats reduces the dominance of single grass and other herbaceous species and can enhance plant community composition (Woodcock & Pywell, 2009). This management technique has been associated with characteristic vegetation composition and specific carabid and other arthropod assemblages (Niemelä *et al.*, 1993; Morris, 2000; Grandchamp *et al.*, 2005; Woodcock *et al.*, 2005b; Middleton *et al.*, 2006), which is supported by the results of this study. However, whilst cutting can enhance the diversity of a beetle community, a reduction in sward height can also result in a loss of key structures normally linked with specific invertebrate communities for feeding or refuge, such as grass tussocks which provide distinguished moisture, temperature and shade characteristics to support a host of specific species (Morris, 2000; Woodcock & Pywell, 2009). The lack of relationship between staphylinid community composition and cutting could be linked to species-specific responses that were not substantial enough to significantly alter community composition. However, as only two sites in this study were subject to cutting regimes (Glaven Farm and Ingworth Bridge), comprehensive conclusions cannot be drawn.

Although grazing and cutting are interlinked in that they both affect the sward height, grazing often results in more selective defoliation, which increases spatial heterogeneity in sward structure and plant species composition (Morris, 2000; Woodcock *et al.*, 2005a). A mosaic of different patches contrasting in plant species and structural heterogeneity within a site can provide more combinations of resources to satisfy the contrasting requirements of different beetle species and therefore increase the diversity and spatial heterogeneity within these assemblages (Dennis *et al.*, 2002). Grazing also indirectly provides additional resources and habitats for beetles such as

dung and carrion (Benstead *et al.*, 1997). However, overgrazing of cattle can completely reduce sward height and plant diversity, subsequently reducing insect diversity (Newton, 2004).

The influence of habitat patch area on beetle assemblage composition has been well documented (e.g. Wiens, 1976; Golden & Crist, 2000; Fournier & Loreau, 2001; Magura *et al.*, 2001a; Ewers *et al.*, 2007; Hendrickx *et al.*, 2007; Gaublomme *et al.*, 2008). It is therefore not surprising that a significant relationship with area was found for both carabid and staphylinid communities in this study. Part of the MacArthur and Wilson's theory of island biogeography (MacArthur & Wilson, 1967), outlines that as habitat areas increase in size, they can provide an increasing number and type of resources and niches for species to exploit, explaining the positive correlation between habitat area and species richness. However, a varied relationship has been demonstrated for beetles. In some studies, small fragments have been shown to host larger numbers of species (e.g. Halme & Niemelä, 1993; Burke & Goulet, 1998), contrary to the theory. Within terrestrial landscapes, habitat 'islands' or patches are surrounded by less hostile environments than 'real' islands, which furthermore commonly host their own beetle species pool (Cook *et al.*, 2002; Lövei *et al.*, 2006). This means that habitat area, as an influencing factor, cannot be wholly differentiated from surrounding landscape composition, pattern and heterogeneity, and edge density (Ewers *et al.*, 2007).

In contrast to community-level responses, at the species level, the effects of area are often more pronounced. Specialist species are commonly limited to large tracts of continuous habitat (Halme & Niemelä, 1993; Usher *et al.*, 1993; Magura *et al.*, 2001a). This is particularly true for forest species that may be reluctant to cross more open habitats (Riecken & Raths, 1996). A number of generalist species dominated in the site assemblages of this study, which may relate to the comparatively small size of habitat patches in the study area. Floodplain habitats in general no longer host large tracts of woodland and fenland (Rackham, 1994; Hammond, 1998; Hughes *et al.*, 2001; Maddock, 2008) and instead are divided into small discreet patches of differing land use types. The size of floodplain habitats along these catchments may therefore no longer be large enough to support high abundances of specialist species.

Landscape variables

With increasingly fragmented landscapes, various elements of the surrounding landscape have been shown to influence beetle diversity of habitat patches (e.g. Burel, 1989; Burke & Goulet, 1998; De La Peña *et al.*, 2003; Aviron *et al.*, 2005; Dauber *et al.*,

2005; Schweiger *et al.*, 2005; Batáry *et al.*, 2007). This study demonstrated that edge density (a measure of exposure to the surrounding landscape), landscape pattern and some surrounding land uses (arable or meadow) influenced carabid and staphylinid assemblages. Habitat edges may exert substantial influence on the spatial distribution of many species, including beetles (Ewers & Didham, 2008). High edge densities have been shown to increase the number of species within a habitat patch because of higher invasion rates from surrounding areas (Halme & Niemelä, 1993; Usher *et al.*, 1993; see also Chapter 3). This intrusion of species from surrounding habitats can increase the diversity of assemblages, but has also been shown to increase the similarity between the focal patch and surrounding matrix (Halme & Niemelä, 1993) thus reducing the prevalence of specialist species (Murcia, 1995; Lövei *et al.*, 2006; Ewers & Didham, 2008). In combination with patch size, the dominance of generalist species across habitat types could be related to the influence of edge density (Lövei *et al.*, 2006). Studies have shown that edge effects commonly impact invertebrate community composition for 100 m into habitats (Ries *et al.*, 2004), but other research on beetles has shown they can penetrate as far as 1km into habitat patches, even for common species (Ewers & Didham, 2008). This indicates that due to the size of the sites studied within this thesis (mean patch size of 7478 m^2), and the remnants of these land use types left throughout the river landscapes, a very strong impact of edge effects may be felt throughout all habitat patches resulting in strongly homogeneous assemblages (Lövei *et al.*, 2006).

Not only do larger edge density ratios increase the potential invasion of species from surrounding habitats, it also results in larger tracts of specific 'edge habitat' or ecotones (Holland *et al.*, 1991), which often host distinct assemblages including 'edge specialists' that require the specific and characteristic light, moisture and microclimate conditions of the respective ecotone (Halme & Niemelä, 1993; Lövei *et al.*, 2006). For example, Buse and Good (1993) found that many staphylinid species favoured forest edges, which therefore hosted species-rich communities, and a similar pattern has been shown for carabid species (Lövei *et al.*, 2006), including a notable preference of *Pterostichus niger* to these edge ecotones. Species-specific associations have become evident in this study. Although limited dispersal (flight) abilities have been shown as the strongest determinant of beetles' response to habitat fragmentation (Den Boer, 1990a; Halme & Niemelä, 1993; Driscoll & Weir, 2005), in this case, *Carabus nemoralis* specimens, which were strongly related to high edge densities, are largely apterous (or brachypterous), whereas *Carabus granulatus*, which were associated with low edge

densities, are macropterous and have been shown to have significant dispersal abilities (Welling, 1990, Figure 4.9). Further analysis into the response of communities to habitat fragmentation using ecological traits will provide stronger causal explanations (Driscoll & Weir, 2005 and addressed in Chapter 6).

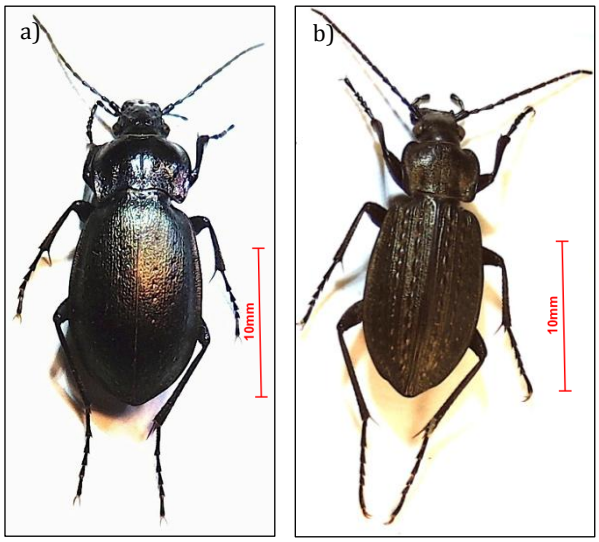


Figure 4.9 Carabid specimens a) Carabus nemoralis *and b)* Carabus granulatus.

Increasing habitat heterogeneity at a landscape scale, and the reduction in dominance by one land use, has the potential to increase species richness as postulated in the habitat heterogeneity hypothesis (MacArthur & Wilson, 1967). This hypothesis assumes that structurally complex habitats provide more niches and ways of resource exploitation and so can increase compositional diversity (MacArthur & Wilson, 1967; Tews *et al.*, 2004). Corresponding to edge density, increased landscape complexity (measured as landscape pattern D_1 within this study) can influence communities by the intrusion of species from a number of surrounding habitats with differing species assemblages to the focal habitat patch. Due to the relatively small scale of sites and patchiness of river landscapes, increased heterogeneity might lead primarily to an increase in the number of widespread generalists, as found in this study. As outlined by Jonsen and Fahrig (1997), increasing landscape diversity means that the number of different habitat types within an area increases, or, that the proportions of habitat types become more equal. This increases the available habitat used by generalist beetles, which may use more than one habitat type to supplement their resources (Dunning *et al.*, 1992). Interestingly, within this study, woodland habitats and their respective assemblages were associated with higher landscape complexity. One could consider that as these floodplain woodland habitats are small remnants positioned

within a landscape of multiple land use types (Hughes *et al.*, 2001), they are more exposed to, and therefore affected by, the surrounding matrix.

Landscape descriptors such as D_1 may not provide a suitable explanation of beetle assemblage composition (e.g. Jeanneret *et al.*, 2003b), in part due to their simplicity in explaining complex landscapes. The composition of surrounding habitat patches, rather than their pattern, has instead been shown to significantly influence beetle assemblages (Jeanneret *et al.*, 2003a; Jeanneret *et al.*, 2003b; Schweiger *et al.*, 2005), largely due to the different species combinations they contribute to the surrounding habitat matrix. Dauber *et al.* (2005) suggest that carabid and staphylinid taxa are more strongly impacted by the composition of the surrounding landscape than other insects, due to their high movement capabilities between landscapes elements. Subsequent resource supplementing and complementing processes from both focal habitat fauna and surrounding habitat fauna is common, which impacts the assemblage composition of both communities (Dunning *et al.*, 1992). Carabids have been shown to be particularly influenced by surrounding cultivated land and woodlands (Jeanneret *et al.*, 2003a; Jeanneret *et al.*, 2003b), and the presence of permanent grassland (De La Peña *et al.*, 2003; Batáry *et al.*, 2007). Staphylinid beetle assemblages may be affected by surrounding arable land as shown in this study, potentially due to higher densities of prey such as aphids, caterpillars and other invertebrates available within arable landscapes (Bohac, 1999). Field margins and adjacent semi-natural habitats can also act as reservoirs for predatory staphylinid species (Pfiffner & Luka, 2000). High dispersal abilities enable them to feed in field margins and take refuge in more natural habitats. A number of species found within this study have commonly been associated with arable landscapes or marginal habitats, including *Lathrobium fulvipenne, Lesteva longelytrata, Omalium rivulare, Philonthus cognatus, Tachinus rufipes, Tachyporus chrysomelinus, Tachyporus hypnorum, Omalium rivulare, Xantholinus linearis* and *Xantholinus longiventris* (Dennis & Wratten, 1991; Krooss & Schaefer, 1998; Bohac, 1999; Pfiffner & Luka, 2000).

Relative influence of habitat and landscape factors

Landscape variables are thought to have an increasing influence on taxonomic assemblages as the landscape is fragmented into increasingly smaller patches progressively more exposed to the influence of the surrounding matrix (Cook *et al.*, 2002). Some studies have suggested that landscape processes can dominate in relative influence over beetle compositions (Aviron *et al.*, 2005; Schweiger *et al.*, 2005). Lawton (1999) suggests that factors at a landscape scale filter and mould local assemblages

because the differences in landscape composition and spatial arrangement influence a regional pool from which local communities are composed. In comparison, local habitat properties support local communities as far as landscape characteristics allow for population dynamics. Thus a top-down hierarchical structure of factors shape local assemblages (Lawton, 1999; Whittaker *et al.*, 2001; Schweiger *et al.*, 2005). Within this research, site factors such as management type still dominated in comparison to the measured landscape influences of pattern, land use and connectivity in shaping carabid and staphylinid assemblages, concurring with a number of other investigations (Jeanneret *et al.*, 2003a; Jeanneret *et al.*, 2003b; Weibull *et al.*, 2003). One explanation is that floodplain environments are known to be highly heterogeneous; even though species and communities are selected from a regional pool, it is the highly complex site scale factors that have the dominant influence (Chapter 5 explores these heterogeneous microhabitat characteristics in floodplain woodlands further). Additionally, a number of key variables that have been shown to influence the diversity of beetle assemblages on floodplains were not measured, including moisture (Bohac, 1999; Dennis *et al.*, 2002; Lassau *et al.*, 2005; Januschke *et al.*, 2011) and sediment type (Sadler *et al.*, 2004; Baiocchi *et al.*, 2012). The inclusion of such factors, and the landscape structure beyond a 250 m radius around the sites, could enhance understanding of the relative influences of site and landscape variables in future work.

Finally, it must be reiterated that the effects of different drivers do not work independently of each other (Dauber *et al.*, 2005). Site area is inexorably linked to edge density and other landscape factors (Golden & Crist, 2000; Lövei *et al.*, 2006; Ewers *et al.*, 2007), and in different catchments and environments, landscape or site scale factors may dominate. Additionally, their impact can be significantly different for different taxa (Golden & Crist, 2000; Jeanneret *et al.*, 2003a; Jeanneret *et al.*, 2003b; Hendrickx *et al.*, 2007). For example, Dauber *et al.* (2005) found surrounding land use to particularly affect carabid beetles in an agricultural landscape in Germany, whereas staphylinids were more strongly affected by local habitat characteristics. Nonetheless, the significance of landscape factors in influencing assemblage composition as identified within this research confirms that they should not be neglected in any investigation into the drivers of beetle community composition.

Spatial distribution of habitats

Recent research has also recognised the importance of geographic distance on biodiversity patterns within a landscape, which in some cases has been shown to have an even greater effect than environmental gradients (Tuomisto & Ruokolainen, 2008;

Baiocchi *et al.*, 2012). This study highlights a significant and strong relationship between staphylinid assemblages and the spatial location of plots. Jeanneret *et al.* (2003b) outline that habitat and landscape descriptors may not explain all aspects of species distribution and composition, as shown in this study. The spatial position of sites can be considered evidence for a number of biotic, abiotic or historic processes that may influence and generate species distribution, and can act as a so-called 'synthetic indirect descriptor of unmeasured factors' (Borcard *et al.*, 1992; Borcard & Legendre, 1994; Jeanneret *et al.*, 2003b). The variation explained by spatial variables displayed in this study indicates that other unmeasured factors may have a role in influencing species compositions and distribution, such as differing flood regimes or geology between catchments, the overall density of particular habitat types or the presence of a larger source area for species in the wider catchment landscape. Furthermore, connectivity measurements and landscape features that have been shown to be important in the structuring of beetle communities, such as hedgerows, were not included in the scope of this research (De La Peña *et al.*, 2003; Fahrig, 2003).

4.4.3 Conservation implications

Cross-taxon conservation strategies

Despite similarities in habitat use, size and a number of ecological traits like trophic position, carabid and staphylinid beetle assemblages were not correlated across sites, habitats or catchments. The importance of considering cross-taxon relationships in biodiversity research and conservation has been well documented (e.g. Noss, 1990; Peres-Neto & Jackson, 2001; Rodrigues & Brooks, 2007; Gioria *et al.*, 2011). Conservation planning and implementation is generally limited by the lack of adequate information about the distribution of biodiversity of a large number of mostly highly diverse taxa (Margules & Pressey, 2000; Scott & Anderson, 2003; Rodrigues & Brooks, 2007). Surrogate taxa that suitably correspond to another taxonomic group in their diversity and distribution patterns can partially address this constraint, somewhat balancing the limited taxonomic expertise, financial, and temporal constraints of 'full' biodiversity surveys (Gioria *et al.*, 2011). This is especially true for staphylinid beetles, for which very limited taxonomic expertise often prevents or hampers studies into the biodiversity of this highly diverse beetle family (Lott & Anderson, 2011).

The effectiveness of one taxonomic group to make inferences about, or predict community patterns of, other taxonomic groups requires first and foremost similar, but independent, responses to the same set of environmental conditions (Rodrigues &

Brooks, 2007). Whilst similar site and landscape factors considered within this investigation were found to impact both carabids and staphylinid beetle assemblages, no direct relationship was established, which may imply contrasting reactions to the same variables (Jeanneret *et al.*, 2003a). Additionally, the spatial location of sites appears to be a considerable factor in driving staphylinid community structure, yet was not significantly influential on carabid assemblages. These considerations indicate that carabid and staphylinid communities may not therefore be suitable as biodiversity surrogates for one another (Rodrigues & Brooks, 2007).

A strong relationship between the community composition of both carabid and staphylinid families and vegetation composition was apparent within this study. Using vegetation as a general indicator for the composition of other taxa is a widespread approach in restoration and conservation practices (Sætersdal *et al.*, 2003). In comparison to the detailed long-term monitoring of large numbers of species needed to detect changes in diversity, especially of mega-diverse taxa (Scott & Anderson, 2003), vegetation surveys are simple, quick and effective. However, the causal mechanisms for this relationship have not been fully explored within this study, and more specific and detailed data would be needed to perform this analysis. This relationship is expected to be non-linear and potentially based on vegetation structure or on environmental parameters such as moisture and shade, to which both assemblages respond (Southwood *et al.*, 1979; Gardner, 1991; McCracken, 1994; Bonn & Kleinwächter, 1999; Blake *et al.*, 2003). Caution must be taken in the use of this relationship for conservation practices and restoration evaluation for the above reasons. In particular for restoration evaluation, Woodcock and McDonald (2010) found that the restoration of beetle assemblages lagged behind the restoration of vegetation within floodplain meadows, largely due to the dispersal limitations of some beetle species within communities.

Importance of staphylinid beetles in research and conservation

The sheer abundance of staphylinid beetles in the ground fauna of these floodplain sites was marked. The dominance of generalist species across habitats in this study does not display the often highly specialised habitat preferences and life histories of staphylinids (Bohac, 1999; Lott, 2003). Staphylinid assemblages can be highly diverse in community composition and show affinity for specific habitat types, and as such staphylinids are considered to be a particularly valuable group for monitoring biological responses to environmental change (Lott & Anderson, 2011). Unique responses of staphylinid communities to site, landscape and spatial factors, in

comparison to carabids, suggest that apposite conclusions about beetle ground fauna and consequent conservation programmes should not be drawn without their consideration.

Conservation of floodplain habitats

Analysis of composition and heterogeneity of beetle assemblages revealed a surprising low overall β-diversity in fen habitats. While floodplain fens have been described as the richest of floodplain habitats in harbouring scarce and threatened arthropod species (Hammond, 1998), consistent management and surrounding landscape changes have meant that many of these habitats are no longer subject to sporadic inundation and have become highly fragmented into small remnants (Purseglove, 1988). This has resulted in potential loss of many species for which floodplain fens are so recognised. The fragmented nature of remaining British floodplain woodlands is also associated with the loss of many specialist species (Buckland & Dinnin, 1993; Drake & Sheppard, 1998; Hammond, 1998). The dominance of generalist beetles within these calcareous fen and floodplain woodland sites suggests that even the most natural floodplains on these rivers may have been, and are being strongly impacted by surrounding landscape change and fragmentation (Jonsen & Fahrig, 1997). Clearly conservation and restoration measures in fragile fen habitats, and floodplain woodlands particularly, need to consider surrounding landscape, edge effects, and conserve wider areas to ensure specialist species and communities can re-colonise and persist in these habitats.

Attention needs to be paid to specific habitat types, yet this study has also shown that a mosaic of different habitats within the landscape has the potential to enhance the beetle communities of river landscapes as a whole. Each management type (meadows, fens and woodlands) provided habitat for different but equally heterogeneous assemblages despite the dominance of generalists, and together could increase the gamma-diversity of floodplain habitats. Conservation practices therefore need to integrate a catchment-scale perspective, not only to incorporate surrounding landscape influences and to warrant that habitat areas are substantial and connected enough to support species sensitive to patch area size, but to ensure different habitat types feature within the overall habitat mosaic. Finally, conservation practices are often classified for broad areas, habitat categories or specific species (e.g. BAP Priority Habitats and Species, Maddock, 2008), and implemented over large scales. This study indicates that floodplains differ from catchment to catchment even over scales of 10km, and consequently conservation measures should be considered for specific catchments and generalisations not made across multiple catchments.

4.5 Conclusion

In Britain the extent and quality of river floodplains has dramatically declined as a result of anthropogenic changes, primarily agricultural and urban expansion. Chalk rivers have been particularly susceptible to these alterations. Despite the potential loss of beetle species associated with changes in these environments (Buckland & Dinnin, 1993; Hammond, 1998) and the dominance of generalists common to all floodplain habitats, this study has shown that distinct beetle assemblages still prevail in chalk floodplain habitats. Site scale factors, primarily management, had a dominant influence on both carabid and staphylinid beetle communities, but this relationship is complex and further complicated by the spatial distribution of sites and habitats, leaving causal factors hard to disentangle.

The outlook for floodplains still involves a dominance of agriculture and pressure of urban expansion, but the increasing recognition of the need to conserve and restore these environments provides momentum for large- and small-scale floodplain restoration (e.g. Peterken & Hughes, 1995; Buijse *et al.*, 2002; Woodcock & McDonald, 2010). Within these practices, cross-taxon and multi-habitat considerations need to be addressed in combination with multi-scale environmental and anthropogenic influences to ensure more substantial and successful ecological outcomes. Additionally, the use of beetle families to inform conservation practices and restoration targets should not be overlooked.

Chapter 5. Micro-spatial distribution of beetles in a chalk stream floodplain forest: implications for conservation and restoration

5.1 Introduction

Floodplain forests have the potential to provide significant ecosystem services, for example in relation to flow regulation, flood prevention, water quality, pollution control, fish production, biological diversity and wildlife habitat (Petts, 1990a; Peterken & Hughes, 1995). Despite their importance, little attention has been paid towards the restoration of floodplain forests in the UK, and information available on their biodiversity is similarly limited (Peterken & Hughes, 1998). Recently, interest in British floodplain forests has increased, but it is still lagging well behind initiatives in continental Europe and North America. The UK Biodiversity Action Plan for wet woodlands (Maddock, 2008), which includes floodplain forests, aims to maintain the total extent and distribution of current wet woodland sites, achieve favourable condition for 80% of these habitats, establish further sites and restore former native wet woodlands to enhance their ability to hold characteristic species.

Due to the prevailing coarse operational scales of conservation and management practices in the UK and globally, conservation and restoration targets are commonly more concerned with habitat area rather than ecosystem functioning. Further, management decisions regarding the environment are made with inadequate knowledge of environmental trends, the state of the environment or its response to anthropogenic influences (Giller & O'Donovan, 2002). Indeed, floodplain conservation initiatives including extensive tree planting have been undertaken by major management agencies such as the Environment Agency with incomplete knowledge (Harper *et al.*, 1997), and no particular benefit to wildlife (Chatters, 2013).

The coarse operational scales of conservation and management are often mirrored in biodiversity studies. Habitat homogenisation, the conversion of heterogeneous

landscapes into single or low diversity patchwork of land uses, is widely recognised as a major threat to biodiversity (Jongman, 2002; Hewitt *et al.*, 2010). The conversion of heterogeneous environments, those with non-uniform, spatial and temporal distribution of resources and abiotic conditions (Addicott *et al.*, 1987), into simple homogenous landscapes has been shown to have strong influences of species and species interactions (McKinney & Lockwood, 1999; Olden, 2006). However, studies regarding its consequences for biodiversity are nonetheless often focussed on broad scales of landscape homogenisation rather than the consequences of small-scale heterogeneity loss (Hewitt *et al.*, 2010). Habitats that appear homogenous to the human eye could have spatial mosaics of different micro-environments, but their role in supporting local species richness is often overlooked (Niemela *et al.*, 1992).

The effects of habitat heterogeneity (synonyms include 'habitat complexity', 'habitat diversity', 'structural heterogeneity' and variations between these) can operate at many scales, and vary considerably depending on the spatio-temporal habitat requirements of the respective species group (Tews *et al.*, 2004). For smaller animals such as beetles, differing resources and abiotic conditions on a metre scale can be considered as habitat heterogeneity, whereas for birds of prey or larger mammals scales of kilometres are more relevant. A microhabitat has been defined as 'the minimum part of the ecohabitat which supplies the requirements of the species in its particular physiological state at that time' (Luff, 1966: 206; Lott, 2003). For the purpose of this study, which is concerned with the distribution of beetles within a floodplain forest site, the term microhabitat will be used to describe differing habitats over scales of less than 10m.

The habitat heterogeneity hypothesis (MacArthur & Wilson, 1967) proposes that an increasing number of habitats leads to an increase in species diversity in a landscape, as structurally complex habitats provide more niches and ways of exploiting environmental resources, reducing competition and allowing for specialisation. For beetles it has been suggested that habitat heterogeneity is required at a small scale due to their complex and specialised habitat requirements, often differing at different stages of life cycles (Stewart & New, 2007). Although local beetle assemblages are inherently linked with the regional pool, the habitat heterogeneity hypothesis suggests that species richness can be greatly increased by heterogeneity within a beetle's activity radius (Niemelä *et al.*, 1996). Habitats with a high complexity of plant characteristics, ground debris and canopy cover have been shown to be linked with high species richness in comparison to low complexity counterparts, often due to

beetle foraging and feeding habits (Lassau *et al.*, 2005). A study of the influence of floodplain forest microhabitats on carabid beetles in Germany found that abiotic and vegetation differences across a floodplain forest strongly influenced the composition and distribution of carabid communities (Antvogel & Bonn, 2001). The fringes of temporary waters were found to be a particularly important habitat for a high number of rare, stenotopic species. However, the affinity of beetle species to certain microhabitats can be difficult to establish as microhabitats may not be independent of each other at small scales and specimens can easily disperse into less favourable habitats from 'source' habitats (Niemela *et al.*, 1992). Significant difference may be found when there is a division of habitats by areas relatively unsuitable for a specific species.

Both carabid and staphylinid beetles have been used in this investigation because they are species-rich families, and are known to be sensitive to environmental change (Lövei & Sunderland, 1996; Rainio & Niemelä, 2003; Gerisch *et al.*, 2006; Luff, 2007; Lott, 2009). The effect of small-scale habitat heterogeneity on carabid beetles has previously been investigated (e.g. Antvogel & Bonn, 2001; Barton *et al.*, 2009). Furthermore, many staphylinids have highly specialised life histories and have been shown to be very sensitive to environmental factors (Bohac, 1999; Lott, 2009), yet have been subject to fewer investigations at the microhabitat scale. In floodplain habitats, some carabid and staphylinid beetles are specifically adapted to microhabitat elements. Areas of standing water may afford unsuitable conditions for some species, yet certain members of the carabid genus *Bembidion*, have legs adapted for swimming, while members of the staphylinid *Stenus* genus have the ability to skim over the water surface by secreting a substance that lowers the surface tension behind them, thus propelling them forward (Lott, 2001, 2003).

Natural and semi-natural floodplain forests can provide a diverse range of terrestrial aquatic and semi-aquatic microhabitats, consequently promoting high biodiversity (Peterken & Hughes, 1995). This large number of microhabitats at the site-scale in floodplain habitats is promoted by disturbance regimes such as flooding and tree fall, fluctuating groundwater tables and a complex micro-topography (Antvogel & Bonn, 2001). With increasing recognition of the potential to restore floodplain woodlands (e.g. Peterken & Hughes, 1995; Sterba *et al.*, 1997; Peterken & Hughes, 1998; Hughes *et al.*, 2001; Berg *et al.*, 2003), and following the recent recognition of wet woodlands as BAP habitats in the UK (Biodiversity Action Plan habitats, Maddock, 2008), there is a growing need to understand these complex environments. Further, to preserve and

enhance the biodiversity of our floodplain forests, it is essential to understand the exact environmental factors that make them suitable for such a diverse range of taxa (Antvogel & Bonn, 2001).

In previous chapters, the importance of different floodplain habitats for beetle communities within chalk river catchments has been recognised, but as communities can change over very limited spatial scales, it is important to also establish and understand the within-site and micro-scale heterogeneity. This chapter therefore investigates the fine-scale characteristics of a single semi-natural but well-established floodplain forest along a chalk river in Norfolk, eastern England, taking the following questions into consideration: (1) Do floodplain forests host heterogeneous habitats at small scales (microhabitats)? (2) Do beetle assemblages vary between the different microhabitats within a floodplain forest? (3) Which abiotic and biotic factors influence beetle assemblages at fine spatial scales?

5.2 Methodology

5.2.1 Study site

Alder Carr is a semi-natural alder- and sycamore- dominated floodplain forest on the upper River Wissey, Norfolk, eastern England (Figure 2.2). The site covers an area of approximately 25,850 m^2 and was chosen for a spatially more detailed investigation because it represents a widely undisturbed, well-established floodplain forest habitat. Alder Carr is owned and controlled by the Ministry of Defence (MoD). It is not accessible by the public, and since its purchase through the MoD, it has been set aside as 'Out of Bounds for Troops'. Aerial photography and historic maps show that it has been wooded since before the 1700s. Furthermore, the site has not been subject to artificial drainage; all channels that flow through the site originate from springs and other calcareous groundwater upwelling within the site. The channels form an island in the middle of the site (Figure 5.10). There is a considerable amount of dead wood on the site due to fallen trees, which have not been cleared or disturbed by humans. A relatively large amount of this dead wood is at a similarly advanced stage of decomposition, which could be attributed to the Great Storm of 1987. The only evidence of human disturbance is found on the riverbanks to the southwest of the site, where remnants of barbed wire fences remain, and a more open habitat with nettle-dominated vegetation cover suggests that a 15-20m stretch of riverbank has been used

for informal fishing. The dominant trees within the forest were *Alnus glutinosa*, *Fraxinus excelsior* and *Acer pseudoplatanus* however a diverse number of tree species were also represented within the forest (Table 5.1).

Table 5.1 Tree species within Alder Carr. Dominant species are marked with a ''.*

Latin name	**Common name**
*Acer pseudoplatanus**	Sycamore
*Alnus glutinosa**	Alder
Buxus sempervirens	Box
Corylus avellana	Hazel
Crataegus monogyna	Hawthorn
Fagus sylvatica	Beech
*Fraxinus excelsior**	Common Ash
Populus x canescens	Grey Poplar
Prunus padus	Bird Cherry
Quercus robur	Pedunculate Oak
Salix alba	White Willow
Salix cinerea	Grey Willow
Salix fragilus	Crack Willow
Ulmus sp.	Elm

Figure 5.1 Alder Carr - view looking east along a side channel through the site. Groundwater springs can be seen as the chalk coloured patches within the water. The channel's source is chalk springs and uprisings at the northeast of the site. The picture was taken in early April so the canopy is moderately open.

Figure 5.2 Examples of fallen trees and dead wood in Alder Carr, River Wissey. These trees are crossing one of the side channels running through the site from chalk springs and uprisings at the northeast of the site.

Figure 5.3 Complex micro-topography within Alder Carr

5.2.2 Field methods

Microhabitat selection

The floodplain forest is characterised by a heterogeneous tree cover including stands of different species, heterogeneous micro-topography, variations in soil moisture, multiple flowing channels and areas of standing water. Consequently, it contains numerous different microhabitats. In order to fully establish the characteristics of the site, it was studied using aerial photographs and by reconnaissance visits where dominant microhabitats were noted and photographed. Six distinctly different microhabitats were recognised based on their micro-topography, soil conditions and vegetation composition and structure as outlined in Table 5.2. Plots of 2 x 2 m were used as sampling units within the forest. With the exception of 'Wooded *Phragmites*' (WP) which was a habitat restricted to the north-eastern edge of the site, plots representing the same microhabitat type were selected across the entire study area to avoid strong spatial correlations with individual habitat types. Each microhabitat category was represented by a minimum of 6 sampling plots. All 45 plots were sampled for beetle and plant species, and key environmental variables.

Table 5.2 Microhabitat categories in Alder Carr

Microhabitat	Code	Characteristics	Number sampled
Understorey Woodland	UW	Shaded areas under dense canopy with limited ground vegetation.	9
Dead Wood	DW	Areas with large concentrations of dead and rotting wood. The majority of dead wood was at advanced decay stages and could be attributed to the Great Storm of 1987.	8
Nettle- and redcurrant/ blackcurrant-dominated	RN	Areas dominated by tall stinging nettle (*Urtica diocia*) and red-/black-currant (*Ribes rubrum*/*nigrum*) plants with simple ground vegetation layering. The dominance of *Ribes* and *Urtica* varied between plots, reflecting the shading caused by tree canopy.	8
Tussock grass-dominated	TG	Areas with open tree canopy where the ground vegetation is dominated by grass tussocks composed of *Brachypodium sylvaticum*.	7
Iris/rush-dominated	IR	Areas with high ground water table characterised by rushes (*Juncus* spp.) and *Iris pseudacorus.*	7
Wooded *Phragmites*	WP	Areas with high ground water table with a canopy of alder (*Alnus glutinosa*) and common reed (*Phragmites australis*) undergrowth, moderately shaded by the comparatively high canopy.	6

Figure 5.4 Understorey woodland plot (UW) in Alder Carr

Figure 5.5 Dead wood plot (DW) in Alder Carr

Figure 5.6 Redcurrant and nettle dominated plot (RN) in Alder Carr

Figure 5.7 Tussock-grass plot (TG) in Alder Carr

Figure 5.8 Iris-rush plot (IR) in Alder Carr

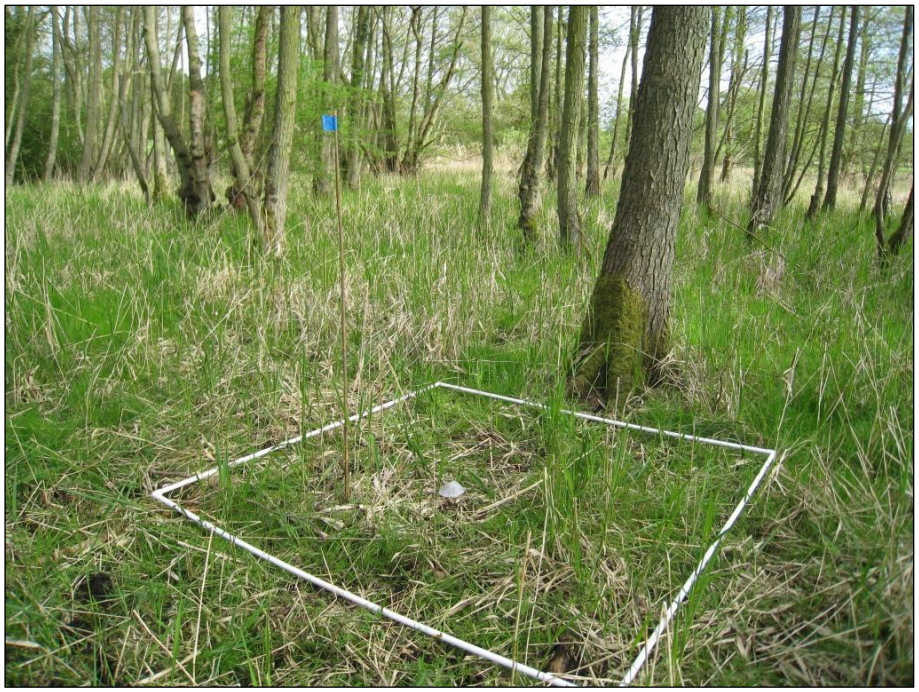


Figure 5.9 Wooded Phragmites plot (PW) in Alder Carr

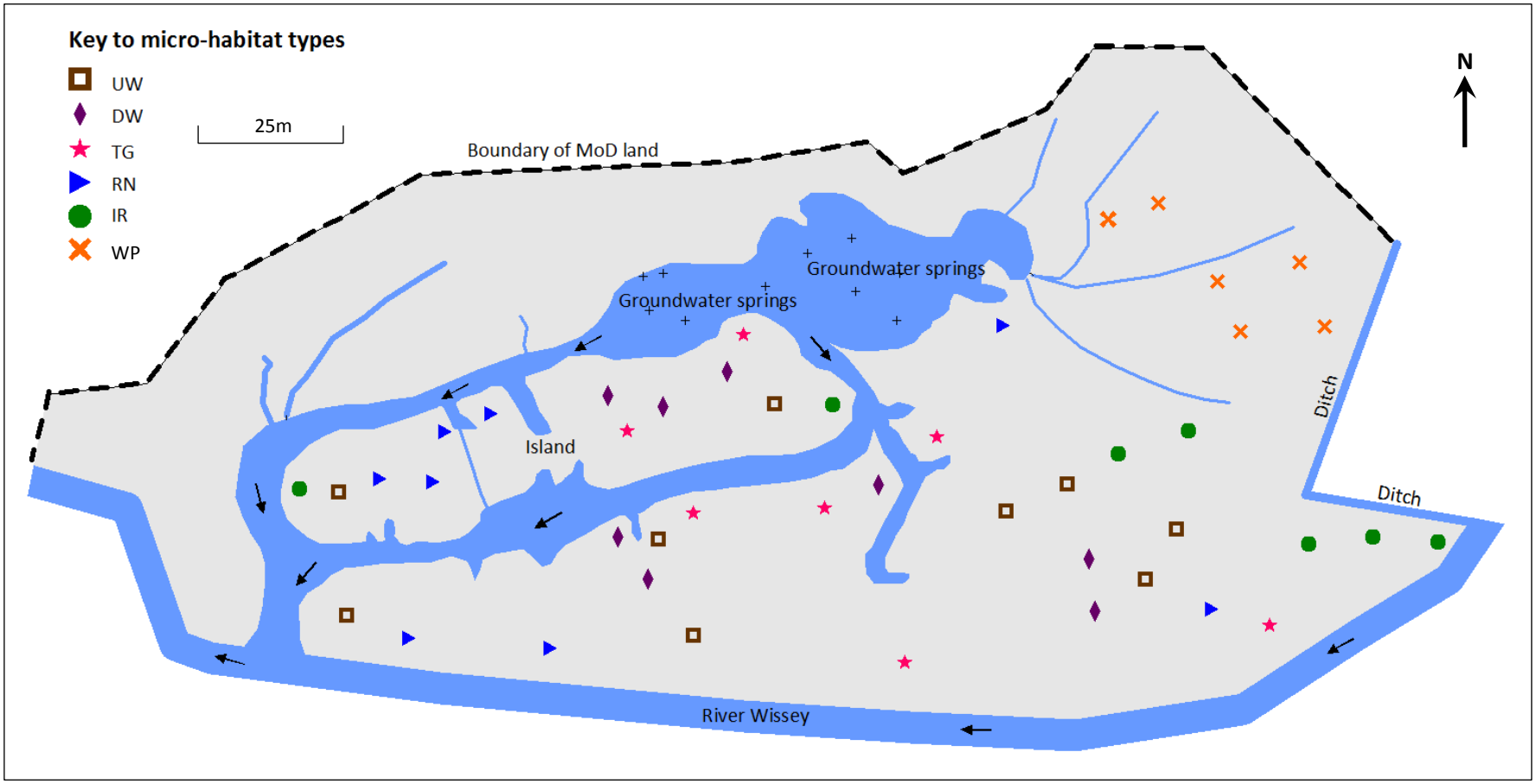


Figure 5.10 Sketch of Alder Carr with microhabitat distribution. Microhabitat codes: DW- Dead Wood; RN- Ribes/Urtica dominated; TG- Tussock Grass; WP- Wooded Phragmites; IR- Iris/Rush dominated; UW- Understorey Woodland

Beetle sampling

Beetles were sampled using a single pitfall trap located at the centre of each 2 x 2 m plot. Holes were dug in the substrate using a corer and plastic cups of 75 mm diameter and 100 mm depth were placed into the holes. Traps were placed level or slightly below the level of the substrate surface to avoid deterrence (Woodcock, 2005), however in areas of severe waterlogging, difficulties arose due to overflowing of traps, which prevented suitable capture of beetles. Each trap was half filled with a preservative solution of 50% IMS and 50% water, with a drop of detergent added to break the surface tension. A non-obstructing cover was placed approximate 40 mm above ground to protect the traps from litter and rain. Traps were left open for two successive weeks from late April to early May (27th April- 11th May 2010) and were emptied weekly. Trap emptying involved the careful removal of slugs, snails, rodents and litter to ensure that no beetles were attached, before partial draining and storage in vials of 70% IMS. A two-week sampling period is a very limited time to interpret the ecological characteristics of a site. However, focusing sampling within a two-week period enabled the detection of species' responses without overdue influence of changing environmental conditions such as flooding and vegetation growth (Antvogel & Bonn, 2001). Additionally, spring is the main activity period for carabid and staphylinid beetles in riparian areas (Lott, 2001) and it has been shown that trapping for a limited time within this period can provide a large proportion of species identified within a full sample season of 28 weeks (Duelli *et al.*, 1990; Jeanneret *et al.*, 2003b).

The limitations of pitfall trapping have been widely discussed in the literature (e.g. Spence & Niemelä, 1994; Woodcock, 2005). For this study, pitfall trapping enabled simple and effective collection of beetles for comparability between microhabitats and plots. Knowledge that abundance figures represent activity density, that is a function of both beetle movement on the soil surface and population density, rather than true abundances (Baars, 1979; Lester & Morrill, 1989), was prominent throughout interpretation of results. Any sample bias towards more active species is likely to be consistent within and between microhabitats allowing for their comparison (Greenwood *et al.*, 1991). However, small-scale complexities in the terrain of certain microhabitats can reduce the mobility of beetle species and therefore should also be considered in the interpretation of results. It is recognised that dead wood, litter and vegetation have the potential to impact sampling efficiency of pitfall traps (Greenslade, 1964; Crist & Wiens, 1995; Sroka & Finch, 2006).

Beetle identification and taxonomy

Beetles were sorted and identified to species-level using keys and reference books (Joy, 1932; Tronquet, 2006; Luff, 2007; Lott, 2009; Lott & Anderson, 2011). Further explanation of identification procedures, including the consultation of reference collections, can be found in Chapter 3.

A number of similar species were grouped, as they are chiefly separable using male genitalia, which only permits the identification of male specimens. For carabid species, these were *Pterostichus nigrita* and *Pterostichus rhaeticus*, which were subsequently grouped into *Pterostichus nigrita* agg. For staphylinid species, *Anotylus sculpturatus* and *Anotylus mutator* were combined as *Anotylus sculpturatus* agg.; *Philonthus micans* and *Philonthus micantoides* were combined as *Philonthus micans* agg.; and *Quedius curtipennis* and *Quedius fuliginosus* were grouped into *Quedius fuliginosus* agg. Species of the Aleocharinae subfamily of Staphylinidae were not identified to species level as described in Chapter 3. Some female specimens of *Gabrius* spp. and *Stenus* spp. (Staphylinidae) were not identified and excluded from the analysis as female specimens were indistinguishable.

Vegetation composition and environmental parameters

Within the 2 x 2 m plot, all vascular plant species were identified to species level (nomenclature followed Hubbard, 1984; Rose *et al.*, 2006; Jermy *et al.*, 2007). In conjunction with assessing vegetation composition for each plot, vegetation structure was also recorded (summarised in Table 5.3). Percentage cover of moss, twigs, dead wood and litter within the plots was recorded along with the maximum and average height of the plants within the plot area. Tree species within a 10 m radius of the plot were recorded, noting the most dominant species using the DAFOR scale (Brodie, 1985). All vegetation data was collected after trapping had been completed in May to ensure minimal disturbance of the plots.

A number of soil parameters were recorded during the beetle-sampling period (summarised in Table 5.3). These measurements were taken at the beginning, middle and end of the beetle-sampling period. Soil moisture levels were recorded using a Delta-T Theta Probe, which approximates volumetric water content (Miller & Gaskin, 1996). As the soil was saturated at most plots, further soil moisture measurements were needed. Small soil samples (approximately 50 x 50 x 50 mm) were taken close to each quadrat, which were frozen between collection and laboratory analysis. Finally,

light intensity was measured at 0, 0.25, 0.5, 0.75 and 1.0 m above the soil surface using a Lux metre on a clear day during the 2-week sampling period.

Table 5.3 Summary of vegetation, soil and microclimate measurements taken at each plot

Environmental Parameter	Description
Vegetation	Cover of all vascular plant species (%)
	Cover moss, twigs, dead wood, litter, bare soil (%)
	Maximum height of plants (m)
	Average height of plants (m)
	Dominant trees within a 10 m radius
Soil characteristics	pH
	Moisture content (%)
	Organic content (%)
Microclimate	Light intensity [lux]

Soil samples were analysed in the laboratory for the characteristics outlined in Table 5.3. Water content was measured as the loss in mass from weighed samples of wet sediment after they have been heated at 105°C for 24 hours. Organic content was determined using the loss-on-ignition (LOI) procedure (Dean, 1974). This involves combusting a known mass of dried sediment at 550°C in a muffle furnace for 2 hours. Organic matter loss was expressed as a percentage of dried sediment. For pH measurements, weighed samples of soil were dissolved into known quantities of buffer solutions (pH7) and pH was measured electrometrically using a Jenway 4320 pH meter.

5.2.3 Statistical analysis

Microhabitat characteristics

Differences in abiotic and biotic characteristics of microhabitats were displayed using a Principal Components Analysis (PCA). The abiotic variables were tested for normality with the use of Shapiro-Wilk normality tests and QQ-plots. Data that did not follow normal distributions were transformed using log transformations. PCA was performed on arc-sine transformed vegetation percentage data, and the first two principal components (as identified by scree plots and correlation analysis) were used as variables representing vegetation species composition in the microhabitat characteristic PCA. Both abiotic and vegetation species data were z-transformed before analysis.

Species composition and alpha diversity

To study differences between beetle abundances and alpha diversity across the microhabitat plots, analysis of variance (ANVOA) was used on counts of collected specimens and Fisher's-α index. Fisher's-α index was calculated for each microhabitat as a measure α-diversity because it has been proven to be sample-size independent (Fisher *et al.*, 1943; Axmacher *et al.*, 2004a; Axmacher *et al.*, 2004b; Liu *et al.*, 2011) and thus a reliable measure of diversity for samples from pitfall traps. The data were then analysed with repeated measures ANOVA to compare differences between microhabitats. Tukey's Honestly Significant Difference (HSD) method was used to investigate pair-wise comparisons between microhabitats. All calculations were performed using R (R Development Core Team, 2011).

Community structure

To visualise the community structure within sites and habitats, an NMDS was used based on a chord-normalised expected species shared (CNESS)-index of dissimilarity matrix. CNESS has been suggested to be one of the most appropriate indices for analysing quantitative data (Trueblood *et al.*, 1994) as it allows for the calculation of probability-based similarity using samples that can differ in sample size (Liu *et al.*, 2010). By varying the sample-size parameter m, the CNESS index of dissimilarity allowed for different analyses with more emphasis on dominant species (smaller values of m) and rare species (larger values of m). This procedure has been used effectively to assess carabid and other arthropod diversity in sites of different management intensities (e.g. Brehm & Fiedler, 2005; Yu *et al.*, 2006; Liu *et al.*, 2010; Michels Jr *et al.*, 2010; Liu *et al.*, 2011). Two values of m were used in this analysis: $m = 1$, and the largest common sample size allowed to ensure at least three plots were represented for each microhabitat type, m=23. Within this analysis, the 'stress' value is the degree to which data in the original space are dissimilar to the distance in the ordination space (McCune *et al.*, 2002). Low stress levels (under 0.2) represent a suitable fit and an accurate visual representation of community dissimilarity, while higher stress values suggest distortion of data (Clarke, 1993). The CNESS dissimilarity matrix was calculated using COMPAH (Gallagher, 1998) and NMDS calculations were performed using R (R Development Core Team, 2011).

Importance of microhabitat characteristics on beetle assemblages

To analyse the potential influence of environmental factors on staphylinid assemblages, a redundancy analysis (RDA) was undertaken. For this purpose, staphylinid data was Hellinger-transformed due to the large number of zero-values in the datasets (Legendre & Gallagher, 2001; Axmacher *et al.*, 2009). PCA was performed on arc-sine transformed vegetation percentage data, and the first two PCs (as identified by scree plots and correlation analysis) were used as variables representing vegetation species composition for the RDA. All variables were z-transformed then tested for co-linearity, and highly correlated variables were removed. An inclusive forward selection procedure was then employed to identify those factors that explained the most variance in staphylinid assemblages. Models were tested using Akaike's Information Criterion (AIC), which is based on goodness of fit (high constrained inertia), but penalises for the number of estimated parameters (Bozdogan, 1987; Oksanen, 2011). The significance of the selected environmental factors was evaluated using Monte Carlo permutation tests (critical $p < 0.01$; permutations = 9999) (Jongman *et al.*, 1995).

Relative importance of abiotic, vegetation and spatial factors on beetle diversity

To analyse the relative importance of abiotic and vegetation factors in structuring the beetle assemblages, a variance partitioning analysis (pRDA) was conducted using Hellinger-transformed beetle species abundances. This approach partitions the total percentage of variation explained by a RDA into unique and common contributions for the sets of specified predictors (Borcard *et al.*, 1992), in this case abiotic, vegetation and spatial variables.

An inclusive forward selection procedure was used on the environmental data (without the PCs representing vegetation composition) to identify those factors explaining the most variation in staphylinid assemblages. A PCA was calculated on arc-sine transformed vegetation data and the first two PCs were used as the second variable for the pRDA. Spatial predictors were constructed using XY coordinates of each plot. Using a Euclidean distance matrix, principal coordinate analysis (PCoA) was conducted and the positive eigenvalues of the PCoA were used as a set of spatial predictors for the third variable in the pRDA.

The pRDA was performed out using 'ape' and 'vegan' packages in R (De Cáceres & Legendre, 2009; R Development Core Team, 2011). The results are given as adjusted R^2 fractions, which are corrected for the number of independent variables in the model (Peres-Neto *et al.*, 2006). The significance of each fraction was tested with 9999

permutations. To enhance the interpretation of plots, the inverse of Simpson's diversity index was calculated for each species across all of the plots. This determines the effective number of occurrences of a species across all plots and when used in an ordination space, gives preference to more dominant species (Oksanen, 2011).

Any causal effects suggested by variance partitioning in this study require proper experimental design and analysis before full conclusions can be drawn (Anderson & Cribble, 1998; Jeanneret *et al.*, 2003b), however within this context, experimental design was not feasible, particularly due to the unique nature of the sampling site.

Species indicative of microhabitats

The presence of species in certain microhabitats can be linked to specific habitat conditions in very specialised species, making them indicators of the presence of these specific conditions. Indicator species analysis was carried out to determine whether certain species were characteristic of each of the classified microhabitats. The indicator value approach (IndVal) was used (Dufrene & Legendre, 1997; De Cáceres *et al.*, 2010), which uses an indicator value index to measure the association between species and site groups representing the microhabitats. The calculation measures the specificity of a species, the probability that the surveyed site belongs to the target site group given the fact that the species has been found, and the fidelity of a species, the probability of finding that species within sites belonging to the specified category (De Cáceres, 2013). The significance of associations was tested using random permutations. This analysis was carried out using the 'indicspecies' package in R (De Cáceres & Legendre, 2009; R Development Core Team, 2011).

Similarity in vegetation and beetle assemblages

As many conservation decisions are made on the basis of vegetation data, Mantel tests were carried out to establish the similarity of vegetation composition, beetle assemblages and the spatial distribution of plots within the site. Mantel tests evaluate correlation between two distance matrices (Legendre & Fortin, 1989), in this case between the staphylinid CNESS dissimilarity matrix (m=1), a Bray-Curtis dissimilarity matrix of the arc-sine transformed vegetation composition data and a Euclidean distance matrix of the XY coordinates for each plot.

Table 5.4 Summary of analytical methods used in Chapter 5

Analytical Method	Application
PCA of abiotic and vegetation species data	To identify the differences in abiotic and biotic characteristics between microhabitat types.
ANOVA between abundance and α-diversity measurements	To assess the differences in beetle α-diversity between microhabitat types.
Non-metric multidimensional scaling (NMDS)	To visualise similarities and differences in beetle assemblage composition across all plots and microhabitat categories.
Redundancy analysis (RDA)	To assess the influence of abiotic and biotic factors on beetle assemblage composition.
Variance partitioning (pRDA)	To establish the relative influence of abiotic, biotic and spatial factors on beetle assemblages.
Indicator Analysis (IndVal)	To identify species associations with certain microhabitat types.
Mantel tests	To determine Assess correlations between beetle assemblages, vegetation composition and the spatial distribution of plots within the forest.

5.3 Results

Microhabitat characteristics

The PCA based on environmental variables in the plots shows a diverse range of microhabitat plots differing in microhabitat environmental characteristics (Figure 5.11). The first two PCs from the vegetation PCA were used to represent vegetation composition in the microhabitat characteristics PCA. They explained the largest proportion of variances in vegetation species composition (Figure 5.12), and high correlation between PC2 and PC3 prevented PC3 from being included.

There is some distinction between microhabitat categories, with separated clustering of the Wooded Phragmites (WP), Understorey Woodland (UW) and Dead Wood (DW) microhabitat plots. UW is characterised by high litter, high percentage cover of twigs, low light levels and low vegetation diversity. DW habitats are characterised by high levels of dead wood, moss and twigs and low pH values. WP habitats are characterised by high moisture, light, vegetation cover and vegetation height. Tussock Grass (TG), Iris Rush (IR) and Redcurrant Nettle microhabitats are less distinctly grouped along the variable gradients.

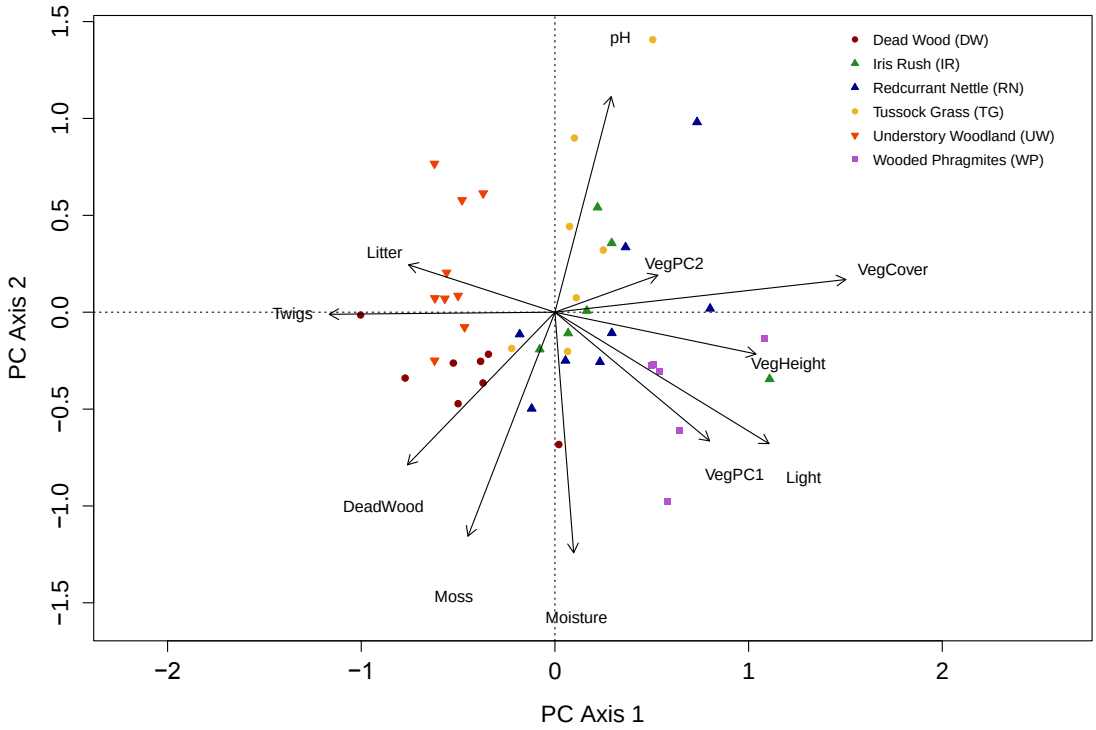


Figure 5.11 Principal Components Analysis of microhabitat characteristics. The variables Veg PC1 and Veg PC2 represent the first principal coordinates of a PCA on vegetation assemblage data. All microhabitat variables were scaled (mean=0, standard deviation=1) before the PCA was performed. Plots are coloured by microhabitat type.

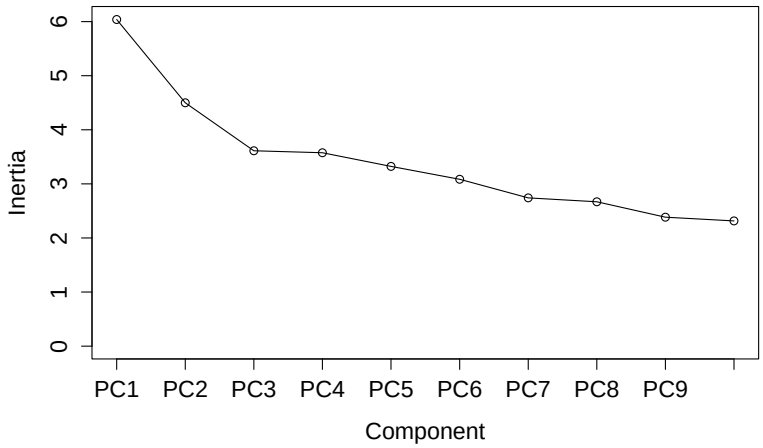


Figure 5.12 Scree plot of inertia explained by each component in a PCA performed on arc-sine transformed vegetation composition data.

Species composition and alpha diversity measurements

One pitfall trap was not recoverable over the two-week period (IR2), due to waterlogging, and so only 44 samples were used in subsequent analyses. A total of 244 carabid beetles and 1027 staphylinid beetles were collected over the two week sampling period and identified to one of 22 and 42 species respectively. A species list can be found in Appendix 7. No carabid specimens were collected in 4 of the 44 pitfall traps (DW3, DW5, DW6 and UW5) and their low overall abundances (n = 244) precluded any comparison in the community composition.

Significant differences in carabid abundances were demonstrated between microhabitat types (Figure 5.13. a). Specifically, *post-hoc* tests indicated significantly greater carabid abundances in UW (mean=9.2) and WP (mean=7.67) compared to DW (mean=1.25), and additionally significantly higher abundances were recorded in UW compared to RN (mean=2.37) (Figure 5.13). In comparison, staphylinid abundances did not differ significantly between microhabitat categories (Figure 5.13. b). Carabid species richness was significantly higher in TG (mean=3.14) and UW microhabitats (mean=3.67) compared to DW microhabitats (mean=1.12), and higher in UW compared to RN (mean=1.87). Other pairwise microhabitat combinations for carabid did not differ significantly and again, staphylinid species richness did not vary significantly between microhabitat types (Figure 5.13. c, d). Fisher's-α was calculated for each individual plot as a measure of species diversity (Figure 5.13. e, f). As no carabid specimens were collected for four traps (DW3, DW5, DW6, UW5), these were excluded from Fisher's-α analyses. High Fisher's-α values were evident for the DW plots (Figure 5.13. e) as few specimens and mainly singletons were collected in these microhabitats, however no significant differences were found between microhabitats for both carabid or staphylinid Fisher's-α calculations.

Correlations between specimen and species counts for each plot, and for abiotic microhabitat characteristics, are shown in Table 5.5. The results suggest that carabid abundances were significantly negatively correlated with percentage cover of moss ($R=-0.362$, $p<0.05$), dead wood ($R=-0.329$, $p<0.05$) and pH ($R=-0.367$, $p<0.05$), carabid species counts were significantly negatively correlated with percentage cover of moss ($R=-0.428$, $p<0.01$). Staphylinid abundances were not correlated with any of the abiotic variables and staphylinid species counts were significantly negatively correlated with percentage cover of dead wood ($R=-0.333$, $p<0.05$) and litter ($R=-0.310$, $p<0.05$) and positively correlated with vegetation cover ($R=0.460$, $p<0.01$).

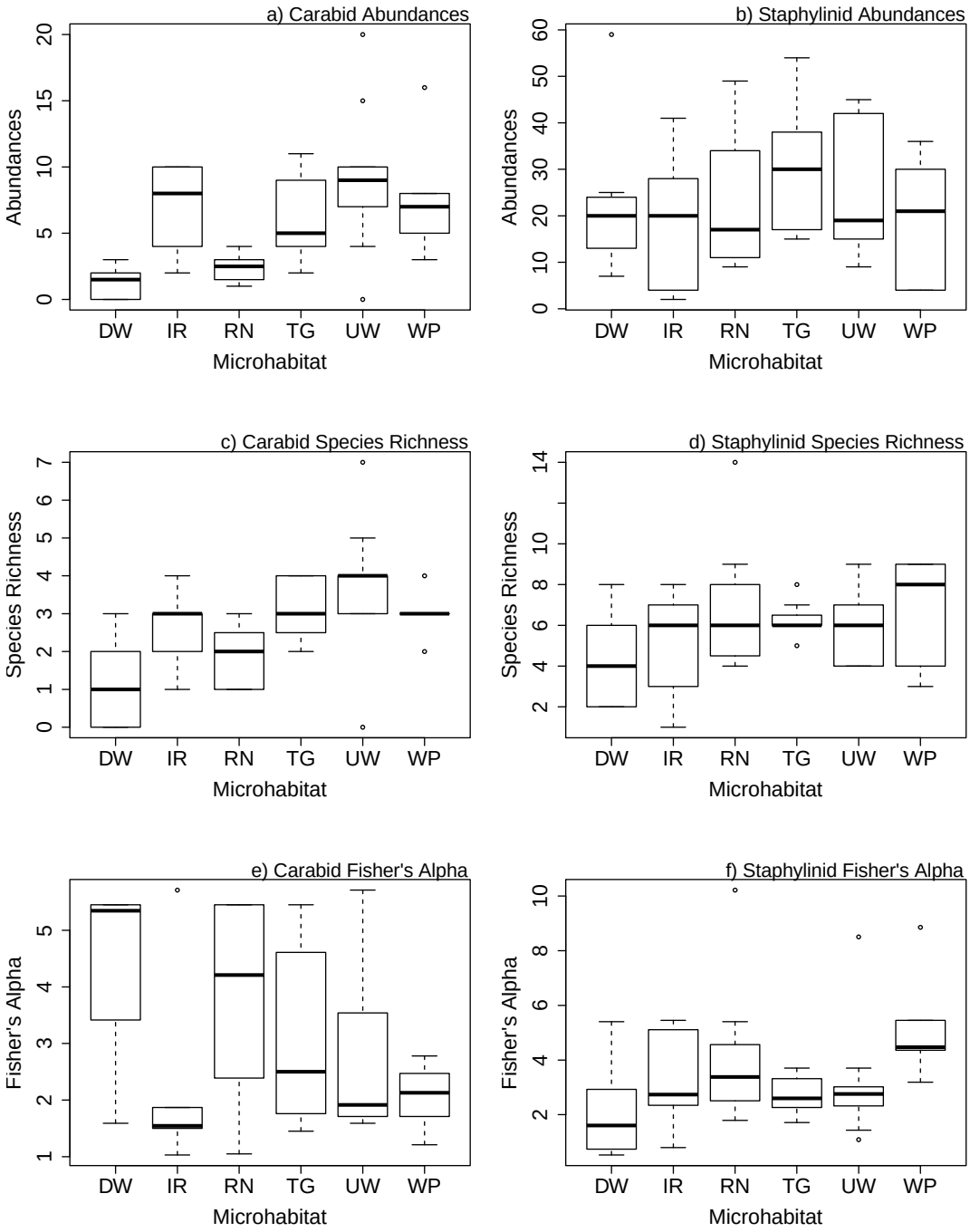


Figure 5.13 Carabid and staphylinid abundances (a, b), species richness (c, d) and Fisher's alpha measurements (e, f) for different microhabitats categories.

*Table 5.5 Pearson correlations between carabid and staphylinid specimen (abundance) and species counts and measured abiotic microhabitat variables. VegPC1 and PC2 are the first two principal components of a PCA on vegetation composition data. Significance for each calculation is shown as '**' <0.01, '*' <0.05.*

	Carabid		Staphylinid	
	Abundances	**Species**	**Abundances**	**Species**
Twigs	0.179	0.199	-0.034	-0.206
Moss	**-0.362***	**-0.428****	-0.290	-0.251
Dead Wood	**-0.329***	-0.271	-0.155	**-0.333***
Litter	0.179	0.064	0.260	**-0.310***
Moisture	0.080	-0.130	-0.153	0.000
pH	**-0.367***	-0.164	0.033	-0.169
Light	-0.016	0.002	0.123	0.226
Veg Cover	0.001	0.094	0.139	**0.460****
Veg Height	-0.066	-0.050	-0.039	0.155
Veg PC1	0.124	0.067	0.170	0.028
Veg PC3	0.283	0.202	0.183	0.054

Community structure

To analyse and visualise differences in staphylinid assemblage structure between the microhabitats, NMDS ordination based on CNESS dissimilarity matrices were performed (Figure 5.14). NMDS stress levels were below 0.2, suggesting a realistic visualisation of dissimilarity in the 2-dimensional NMDS in comparison to the calculated CNESS dissimilarity matrix. When dominant species are considered (m=1), the microhabitats are clustered and overlapping, due to similarity in common species abundances (Figure 5.14.a). However, WP plots still display some distinction. When taking into account rare species (m=23), there were more distinct differences in microhabitat staphylinid communities across the microhabitats (Figure 5.14.b), although considerable overlap was also evident. Microhabitats WP, TG and UW in particular suggest more distinctive species assemblages, whereas DW, RN and IR are less definite. NMDS using CNESS does not allow for the incorporation of species scores in analysis.

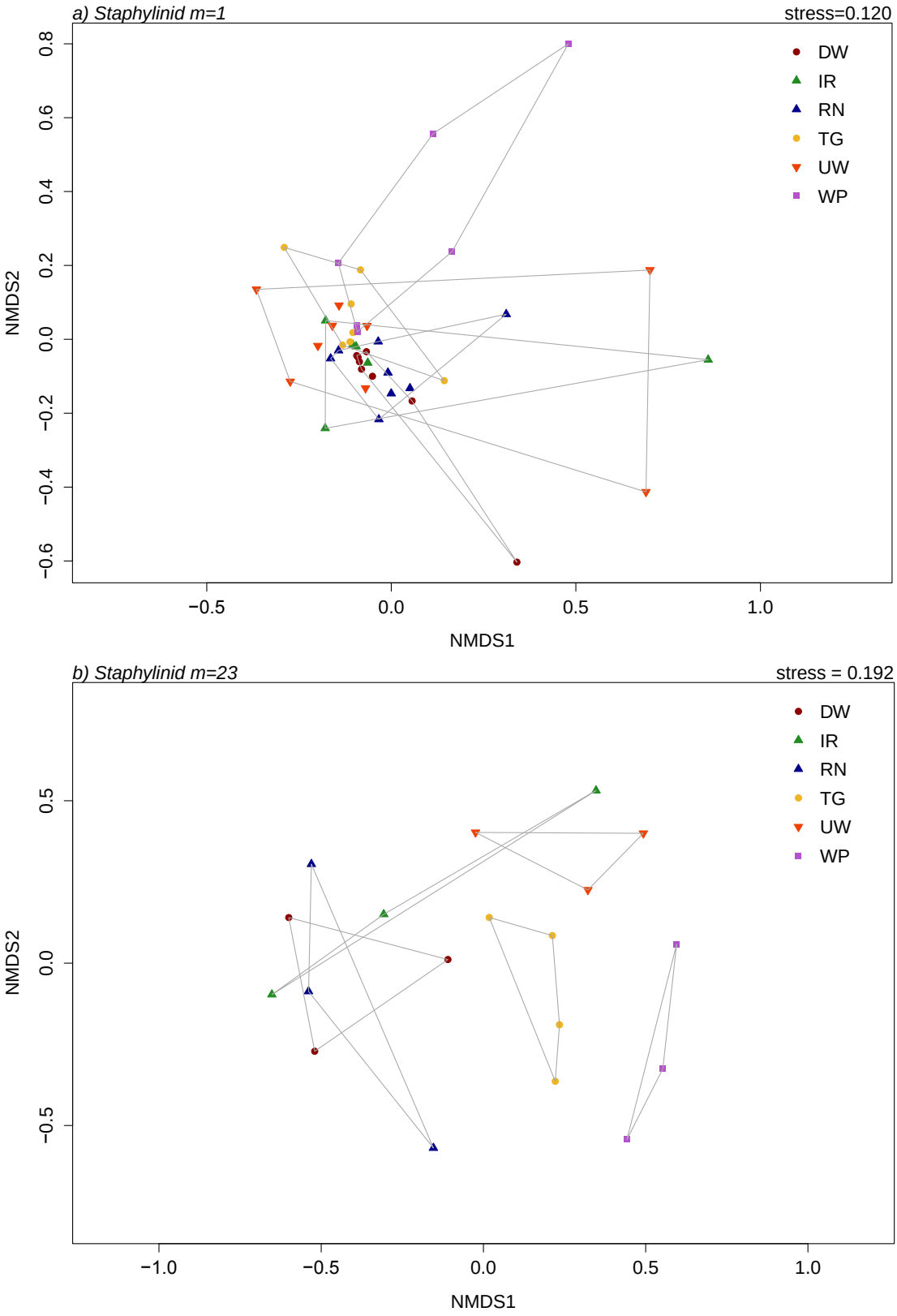


Figure 5.14 Non-metric multidimensional scaling (NMDS) ordination showing differences in staphylinid assemblages using CNESS dissimilarity matrices for m=1, and m=23. Plots are coloured according to microhabitat. Less plots are included in (b) as this only includes plots with 23 specimens or more. Stress levels represent the degree to which the NMDS reflects the calculated dissimilarity matrix. Lower values (<0.2) represent more suitable fitting of data.

Importance of microhabitat characteristics on beetle assemblages

Bare soil cover (%) was highly correlated with both vegetation cover and vegetation assemblage composition so was removed from further ordination analyses. For similar reasons, average height of plants (m) was used and maximum height of plants (m) omitted. Soil moisture was highly correlated with organic content, and as it is highly related to short-term weather fluctuations, soil moisture was excluded from the RDA. To establish the significance of both the abiotic variables and vegetation composition in explaining staphylinid assemblages across the site, an RDA was run on the z-transformed environment data (Table 5.6). Vegetation composition (the first two principal components for the vegetation PCA – Veg PC1 and Veg PC2) was significant in explaining variance in staphylinid assemblages, as was dead wood cover, twig cover and light (all $p < 0.05$).

*Table 5.6 Significance of abiotic variables and vegetation composition in explaining the variation of staphylinid assemblages in a Redundancy Analysis (RDA) full model. Significance for each calculation is shown as '**' <0.01, '*' <0.05.*

Environmental Parameter	F-Value	P-Value
Vegetation cover (%)	0.765	0.66
Average vegetation height (m)	1.003	0.45
Vegetation composition PC1	**2.383**	**0.02***
Vegetation composition PC2	**2.113**	**0.03***
Dead wood (%)	**1.960**	**0.01***
Litter (%)	0.688	0.75
Moss (%)	1.740	0.09
Twigs (%)	**2.235**	**0.03***
pH	1.067	0.35
Organic Content (%)	1.021	0.40
Light (lux)	**2.077**	**0.02 ***

The best model using stepwise forward selection included vegetation composition (Veg PC1 and Veg PC2), dead wood (%) and twigs (%). This model explained 20.5% of the variance in the data with an AIC value of -39.23 and a significance of $p<0.01$. Plots differ in species assemblages across the environmental gradients (Figure 5.15), however there is some clustering of assemblages according to microhabitat type such as UW, DW and WP plots. A number of species are clustered around the centre of the ordination diagram (including *Anotylus rugosus, Carpelimus elongatulus, Gabrius trossulus, Lathrobium brunnipes, Omalium rivulare, Philonthus intermedis, Xantholinus linearis*), suggesting the prevalence of generalist species or species preferring intermediate environmental conditions.

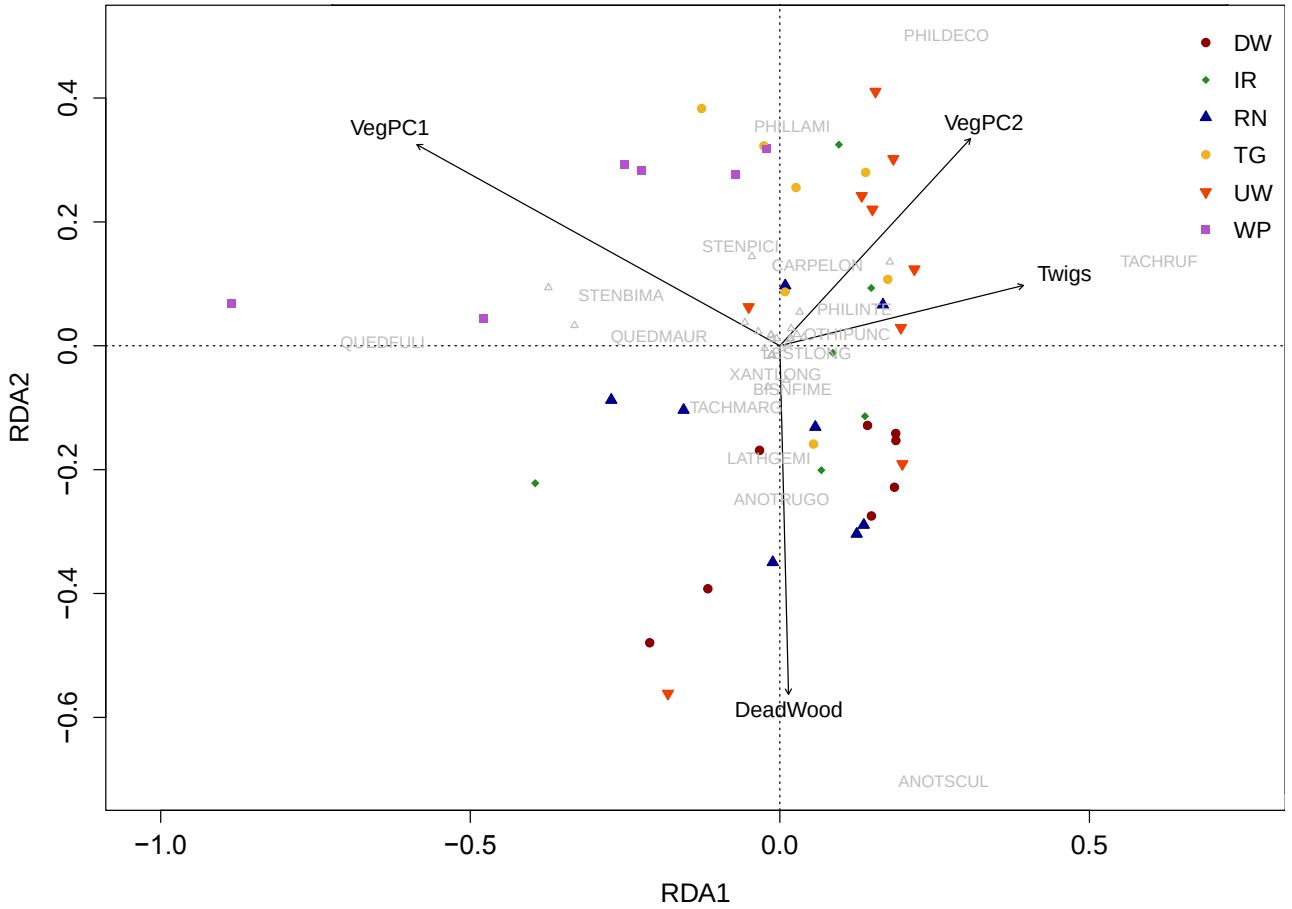


Figure 5.15 Redundancy analysis (RDA) of staphylinid assemblages in relation to microhabitat variables. Forward selection identified vegetation composition (VegPC1 and VegPC2), dead wood cover and twig cover as significant variables (shown by arrows). Plots are coloured according to microhabitat type (see Table 5.2 for microhabitat abbreviations). Species names are abbreviated (see Appendix 7 for a full list of species' abbreviations). Species labelling priority is given to the most abundant species using the inverse of Simpson's diversity index. Rarer species not labelled are marked as an open triangle.

Variance partitioning analysis (pRDA) revealed a dominant influence of vegetation on staphylinid assemblages across the floodplain forest. Total adjusted variability in staphylinid assemblages explained by environmental variables, vegetation composition and spatial proximity components together was 18%. Abiotic variables, after conditioning for vegetation and the spatial factor [A|VS], explained 4% of adjusted variation in the staphylinid assemblages. Vegetation, after conditioning for the abiotic and spatial factors [V|AS], explained 8% of adjusted variation. Spatial factors, after conditioning for the abiotic and vegetation factors [S|AV], explained 6% of adjusted variation. Over 80% of the variation in the staphylinid assemblages was not explained by these factors.

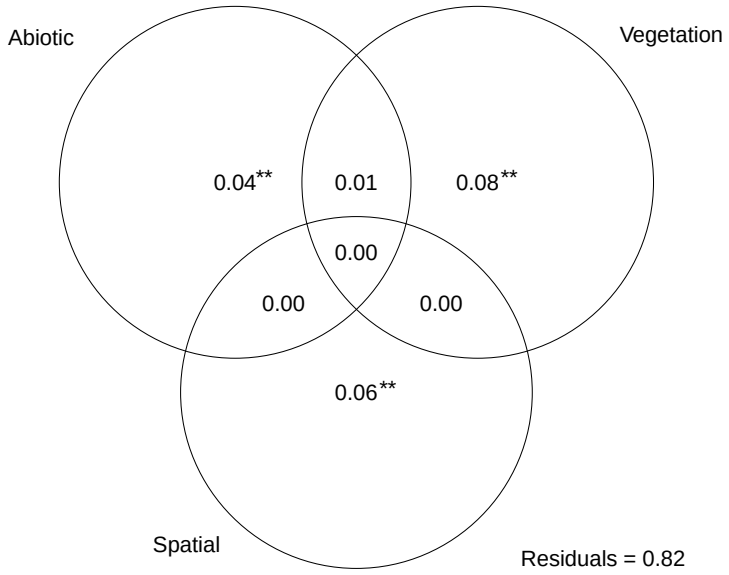


*Figure 5.16 Variance partitioning of the relative influence of abiotic variables, vegetation and spatial location on carabid assemblage composition within this site. Values represent the proportion of the adjusted variation (total = 1), which have been rounded to 2 decimal places. Significance for each calculation is shown as '**' <0.01, '*' <0.05.*

Indicator species results

No species was found to be completely distinctive of a single habitat and not found in another (A>0.95, B>0.95, Table 5.7.). However, eight species were found to be significant indicators of microhabitat groups (p<0.05). *Anotylus sculpturatus* agg. was indicative of DW microhabitats (stat=0.635, p<0.01), *Philonthus laminatus* of TG habitats (stat=0.613, p<0.05), and *Lesteva longoelytrata* and *Othius punctulatus* were indicative of UW microhabitats (stat=0.577 p<0.05 and stat=0.576, p<0.05 respectively). *Stenus juno* (stat=0.577, p<0.05), *Stenus picipes* (stat=0.577, p<0.05), *Quedius fuliginosus* (stat=0.667, p<0.01) and *Lathrobium brunnipes* (stat=0.533, p<0.05) were all indicative of WP microhabitats. The results indicated that no species were significantly distinctive to the IR and RN microhabitats alone.

Table 5.7 Indicator species for microhabitats. 'A' represents the IndVal statistic for specificity and 'B' represents the IndVal statistic for fidelity. Pictures of each species are given in Figure 5.17.

Microhabitat	Species	A	B	Indicator statistic	p value
DW	*Anotylus sculpturatus* agg.	0.4033	1.000	**0.635**	0.008
IR	-				
RN	-				
TG	*Philonthus laminatus*	0.5265	0.7143	**0.613**	0.016
UW	*Lesteva longoelytrata*	1.000	0.333	**0.577**	0.028
	Othius punctulatus	0.5970	0.555	**0.576**	0.016
WP	*Quedius fuliginosus*	0.4450	1.0000	**0.667**	0.002
	Stenus juno	1.0000	0.3333	**0.577**	0.038
	Lathrobium brunnipes	0.5688	0.5000	**0.533**	0.037
	Stenus picipes	0.8182	0.3333	**0.522**	0.046

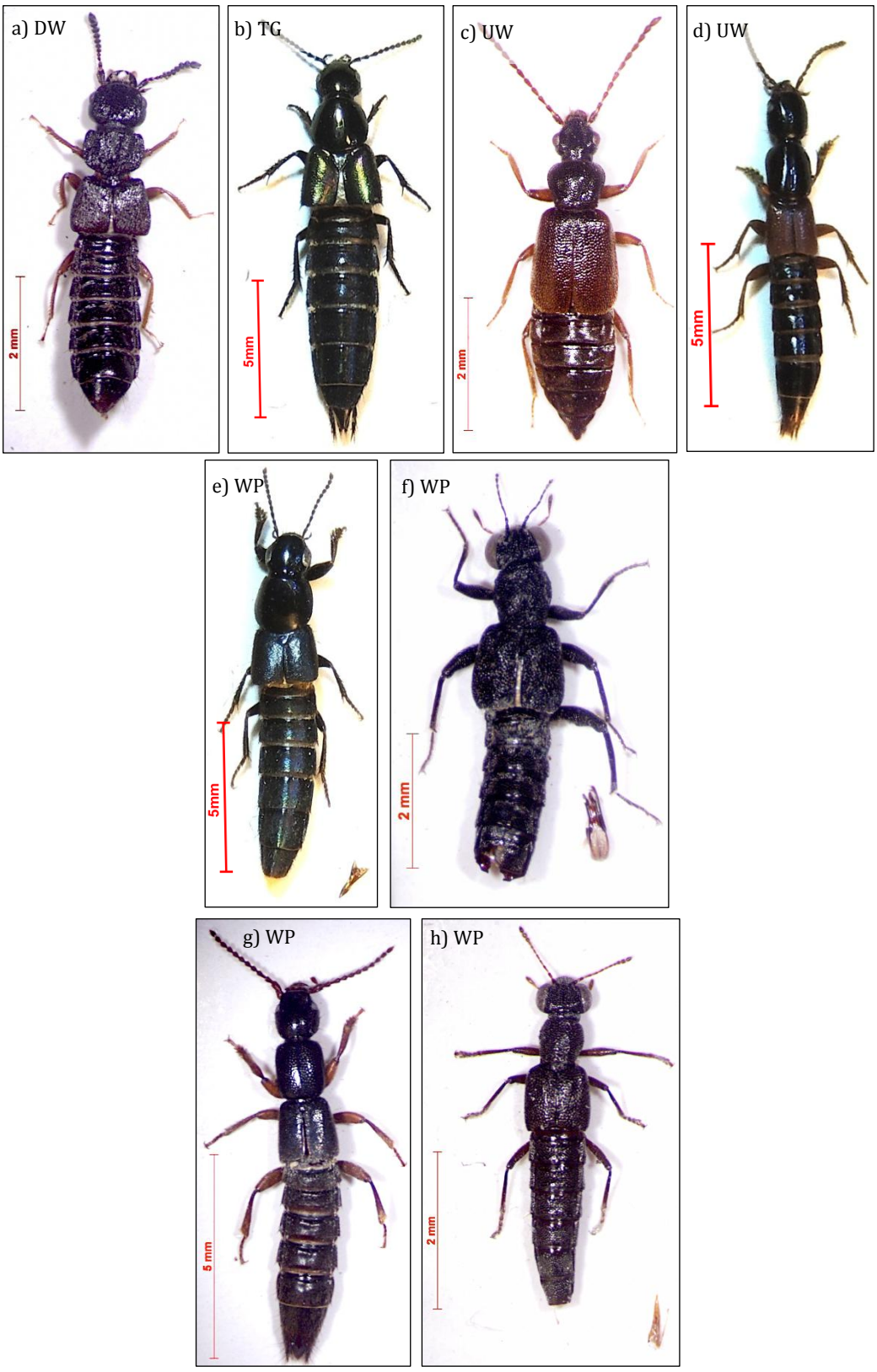


Figure 5.17 Pictures of species indicative of microhabitats: a) DW - Anotylus sculpturatus *agg., b) TG* - Philonthus laminatus, *c) UW* - Lesteva longoelytrata, *d) UW* - Othius punctulatus, *e)* Quedius fuliginosus *(dissected to reveal genetalia), f) WP* - Stenus juno *(dissected), g) WP* - Lathrobium brunnipes *and h) WP* - Stenus picipes *(dissected)*

Mantel tests confirmed a strong relationship between assemblages and spatial distribution of plots (R=0.265, p=<0.01; Table 5.8). A significant correlation between staphylinid assemblages and vegetation composition was also evident (R=0.139, p<0.05) however, when the spatial component was excluded in a partial Mantel test, this relationship was no longer significant. Additional tests between vegetation and the spatial distribution of plots were significant, suggesting a distinct distribution of microhabitat groups across the site differing in both vegetation composition and staphylinid assemblages. The relationship between spatial and vegetation components was stronger and more significant when the abiotic component was excluded (R=0.283, p<0.01).

Table 5.8 Mantel and partial Mantel results between staphylinid communities (CNESS dissimilarity matrix), vegetation communities (Bray-Curtis dissimilarity matrix) and the spatial dataset (Euclidean dissimilarity matrix). No data was transformed prior to analysis and Mantel tests were run for 9999 permutations. R represents the correlation between the dataset using the Pearson statistic.

Mantel Test	**R**	**P**
Staphylinid and vegetation	**0.139**	**0.029**
Staphylinid and abiotic environment	-0.034	0.593
Staphylinid and spatial	**0.265**	**0.001**
Spatial and vegetation	**0.119**	**0.027**
Spatial and abiotic environment	0.095	0.070
Partial Mantel		
Staphylinid and vegetation excluding any spatial component	0.067	0.157
Staphylinid and vegetation excluding any abiotic environment component	**0.144**	**0.025**
Staphylinid and abiotic environment excluding any spatial component	-0.062	0.703
Staphylinid and abiotic environment excluding any vegetation component	0.051	0.670
Spatial and vegetation excluding any abiotic environment component	**0.283**	**<0.001**
Spatial and abiotic environment excluding any vegetation component	0.063	0.152

5.4 Discussion

5.4.1 Variation in beetle assemblages across different microhabitats

The results suggest a lack of distinction in staphylinid beetle assemblages between microhabitat types. Contrastingly, differences in species diversity and assemblage structure have been shown between different characteristic small-scale habitats for carabid beetles (Niemela *et al.*, 1992; Koivula *et al.*, 1999; Antvogel & Bonn, 2001; Brose, 2003a; Barton *et al.*, 2009), other beetle families (Wiens & Milne, 1989; Lassau *et al.*, 2005; Apigian *et al.*, 2006; Janssen *et al.*, 2009), and other arthropods (Niemelä *et al.*, 1996; González-Megías *et al.*, 2007; Foord *et al.*, 2008). The lack of specificity of staphylinid species and assemblages to specific microhabitat categories within this study could be attributable to the high abundance of generalist species. Lassau *et al.* (2005) found little evidence of staphylinid species specificity to forest microhabitats, primarily due to the association of generalists to a number of habitat characteristics that may be provided by a collection of different microhabitats. The results of this study demonstrated little distinction between microhabitats when common species were considered, yet clearer distinctions when rare species were included, suggesting a dominance of species that occur across multiple microhabitat types.

The activity patterns and radii of beetle movement through the fine microhabitat matrix may also have reduced the distinction between microhabitat types. The trapping method used in this study attributes each specimen to the microhabitat within which it was trapped, regardless of whether that is its main habitat or whether the beetle was only migrating through the respective habitat patch. Niemela *et al.* (1992) similarly pointed out the difficulty in 'proving' the affinity of beetles to certain microhabitats due to their dispersal into less favourable habitats from the 'source' habitat for hunting and foraging purposes. At very fine spatial scales, distribution and abundances of beetle species are heavily influenced by movement of individuals through the habitat mosaic in combination with foraging strategies and response to interacting physical and biotic factors (Hassell & Southwood, 1978; Niemela *et al.*, 1992; Wallin & Ekbom, 1994; Firle *et al.*, 1998). Additionally, the significant relationship between staphylinid assemblages and the spatial distribution of sampling plots both in variance partitioning analysis and Mantel tests suggests that species may be associated with larger areas within which specific combinations of resources are available, rather than being defined to small-scale microhabitats. The range at which beetles forage, identify suitable habitats and disperse is strongly dependent on an

individual species' feeding habits and flight abilities. Dispersal abilities have often been stated as the main cause for spatial patterns in diversity across fragmented landscapes (Økland *et al.*, 1996; Rykken *et al.*, 2011). At finer spatial scales, however, there is little research into this relationship, potentially as the majority of staphylinid species can fly and disperse relatively easily across small study areas (Tottenham, 1954). The range at which species utilise resources combined with the inter-dispersed distribution of microhabitat types throughout the site could therefore be a strong driver of the observed trends in staphylinid beetle assemblage compositions across this floodplain forest.

Notably, the sampling period may have further reduced distinctions between microhabitat types. A two-week sampling period can be considered a limited time to interpret the ecological characteristics of a site. However, focusing sampling within a two-week period enabled the detection of species' responses to vegetation and abiotic gradients without overdue influence of changing environmental conditions such as flooding and vegetation growth (Antvogel & Bonn, 2001). Additionally, spring is suggested to be the main activity period for both carabid and staphylinid beetles in riparian areas (Lott, 2001), and it has been shown that trapping for a limited time within this period can provide a large proportion of species identified within a full sample season of 28 weeks (Duelli *et al.*, 1990; Jeanneret *et al.*, 2003b). However, the limited presence of large *Carabus* species from the dataset is notable. Such species are characteristic autumn-breeders and more active within autumnal months. A year-long sampling strategy could potentially identify whether seasonal differences reveal more distinguished assemblages, in particular between microhabitat types. However, such an approach is likely to reduce the interpretability of community and species responses to abiotic and vegetation factors as outlined above.

5.4.2 Influence of abiotic and vegetation factors on beetle assemblages

A number of microhabitat studies have investigated the influence of abiotic gradients on carabid beetles (e.g. Niemela *et al.*, 1992; Niemelä *et al.*, 1996; Koivula *et al.*, 1999; Antvogel & Bonn, 2001; Heliölä *et al.*, 2001; Barton *et al.*, 2009), whereas few studies have considered staphylinid beetles (Kappes & Topp, 2004; Lassau *et al.*, 2005; Apigian *et al.*, 2006; Janssen *et al.*, 2009). While distinction between pre-defined microhabitat types was not marked within this study, staphylinid beetles responded to a number of abiotic and vegetation gradients at the microhabitat scale.

The negative association of staphylinid beetles with dead wood strongly contrasts with previous research. Staphylinid beetles often predate on deadwood invertebrates, and therefore, high numbers have been associated with dead wood habitats (Kappes & Topp, 2004; Lott, 2009; Lott & Anderson, 2011). A potential reason for the diverging patterns found at the River Wissey could be a low presence of saproxylic species in the local species pool. Saproxylic species are those that depend, during some part of their life-cycle on dead or dying wood (Speight, 1989; Siitonen, 1994). *Anotylus sculpturatus* agg. (Figure 5.18), a detritivorous species associated with dead wood, was the only species known to be associated with high levels of dead wood and characteristic to dead wood microhabitats present in the respective samples. Further analysis into the feeding habits of the beetles identified within dead wood plots and the remaining microhabitats would reveal if other saproxylic beetles showed associations to specific habitats.

Figure 5.18 Anotylus sculpturatus *agg., a detritivorous species associated with dead wood microhabitats within Alder Carr.*

Secondly, the stage of decay and the continuity of dead wood throughout a habitat have both been found to be important factors in determining the saproxylic beetle species diversity within dead wood microhabitats (Økland *et al.*, 1996; Martikainen *et al.*, 2000; Schiegg, 2000; Similä *et al.*, 2003). As the majority of dead wood within the River Wissey site can be attributed to the Great Storm of 1987, the age and level of decay were high, which may have impacted the presence and abundance of saproxylic staphylinid and carabid species across the site. Saproxylic beetles have also shown strong responses to the spatial arrangement of dead wood, with high dead wood connectivity promoting higher abundances of a number of saproxylic species (Schiegg,

2000). The physical spread of dead wood throughout the site therefore may have further influenced the presence of these species and the overall association of staphylinid beetles with dead wood.

Lastly, dead wood can impact the efficiency of pitfall trapping methods by reducing mobility and therefore the likelihood of capture (Greenslade, 1964; Crist & Wiens, 1995; Sroka & Finch, 2006). A limited relationship between carabid beetles and dead wood has previously been attributed to trapping methods because carabid beetles are generally more active or inactive (depending on the season and life-stage) underneath the bark of the decaying wood, which can therefore reduce the trapping potential of ground-level pitfall traps (Antvogel & Bonn, 2001). This may have had an impact on the samples within dead wood microhabitats.

In addition to dead wood, the negative relationship identified between staphylinid species and percentage cover of litter was unexpected. About half of staphylinid species are found in litter (Bohac, 1999; Lott, 2009; Lott & Anderson, 2011), and their elongated and flexible bodies are ideal for weaving through this medium. It could therefore be expected that they show a high abundances and species richness within microhabitats covered with dense leaf litter. Leaf litter has been found to affect invertebrate distributions both directly and indirectly (Facelli & Pickett, 1991; Niemela *et al.*, 1992; Koivula *et al.*, 1999; Antvogel & Bonn, 2001); not only can it provide shelter from adverse microclimatic conditions and from predators, but it also constitutes a favourable medium for foraging (Koivula *et al.*, 1999). However, these relationships have been closely related to the feeding habits of staphylinid species, for example detritivorous *Oxytelinae* spp. have been closely linked with litter habitats (Lassau *et al.*, 2005). Further analysis to explore the relationships between feeding guild and microhabitats association is presented in Chapter 6.

Strong relationships found between vegetation and staphylinid beetle species richness and composition can be linked to a number of causal theories. Firstly, the 'taxonomic diversity hypothesis' suggests that taxonomic diversity of plant species is directly correlated with the diversity of herbivores, as each additional type of resource can support further, specialised consumers (Murdoch *et al.*, 1972; Prendergast *et al.*, 1993; Siemann, 1998; Siemann *et al.*, 1998; Brose, 2003a), thereby also facilitating higher diversities in predators and parasites (Hunter & Price, 1992; Siemann, 1998; Siemann *et al.*, 1998). Vegetation composition has been identified as the most effective predictor of arthropod assemblage composition across a range of species groups including

carabids (Schaffers *et al.*, 2008). However, studies into the direct link between vegetation composition and staphylinid assemblage composition are limited.

Alternatively, the relationship demonstrated between vegetation cover and staphylinid species richness and community composition could be linked to the 'structural/habitat heterogeneity hypothesis', which assumes that structurally complex habitats may provide more niches and ways of exploiting resources than homogenous habitats (Southwood *et al.*, 1979; Tews *et al.*, 2004). Testing the relative importance of vegetation composition and structural heterogeneity in wetland environments, Brose (2003) found structural heterogeneity of the vegetation to be the most important predictor variable for carabid species richness. For carabids, some studies have suggested that vegetation structure and cover and its subsequent influence on microclimate and food sources is one of the most important factors affecting the distribution of carabid species (Niemela *et al.*, 1992; Magura *et al.*, 2000; Magura *et al.*, 2001b; Frank & Reichhart, 2004). For staphylinid beetles, the structure and percentage cover of vegetation has been shown not to impact assemblages as a whole, but rather exert influence on certain staphylinid subfamilies (Lassau *et al.*, 2005). Fungus-feeding Scaphidiinae spp. have been associated with higher percentages of herb cover, whereas limited relationships with vegetation cover have been identified for predatory Staphylininae, Paederinae and Pselaphinae subfamilies (Lassau *et al.*, 2005).

Finally, it has been argued that correlations between plant and beetle assemblages more specifically reflect abiotic factors that influence the composition in both groups (Andersen, 1983; McCracken, 1994; Bonn & Kleinwächter, 1999; Blake *et al.*, 2003). Staphylinid beetles have been suggested to hold only loose plant associations and are instead primarily associated with microhabitat moisture properties (Hammond, 2003), to which plants may also be responding.

All of these hypothesis and explanations are inevitably interlinked; as each plant species has its own specific architecture, a strong relationship exists between plant species composition and vegetation structure (Schaffers *et al.*, 2008). In turn, vegetation structures also impact on microclimatic conditions. In addition, the strong influence of microhabitat-scale environmental conditions on vegetation species is well known (e.g. Ellenberg, 1988; Grime, 2001). These three entwined explanatory relationships cannot be untangled reasonably in this context to outline and delineate the specific influence of vegetation on staphylinid species composition within this study.

As suggested here, single species and species grouped by functional traits can show stronger responses to environmental gradients than communities as a whole (e.g. Nield, 1976; Andersen, 1983; Rushton *et al.*, 1991; Niemela *et al.*, 1992; Wallin & Ekbom, 1994; Økland *et al.*, 1996; Koivula *et al.*, 1999; Betz, 2002; Magura, 2002; Lassau *et al.*, 2005). This may explain some of the weak or missing correlations between environmental variables and species composition defined by taxonomy in this study. Some authors suggest that species distribution of carabids is governed solely by the availability of food (Loreau, 1986; Szyszko, 1996), providing more distinct groupings by feeding guild. Mycophagous (fungus-eating) species have been shown to be more highly associated with microhabitats in comparison to predatory species that may utilize a greater range of habitats whilst foraging because they are generally more active during feeding (Lassau *et al.*, 2005). Analysis of the same data by trait groupings (addressed in Chapter 6) or more detailed analysis of indicator species may provide stronger explanations to micro-spatial distributions of both carabid and staphylinid beetles across this floodplain forest.

5.4.3 Conservation implications

Some important conservation implications can be drawn from this research: the importance of addressing floodplain management at multiple scales; the importance of microhabitat heterogeneity within floodplain forests; the potential for restoration of floodplain forests in Britain; and consideration of the relationship between beetles and vegetation in conservation and restoration activities.

Research into the associations between biodiversity and habitat heterogeneity is often motivated by a desire to generalise ecological patterns at human-landscape scales (Lassau *et al.*, 2005; Hewitt *et al.*, 2010), and studies are largely linked to the scales at which conservation practices are applicable, namely local site and regional scales. Diversity is scale dependent (Magurran, 2004; Janssen *et al.*, 2009) and it is important to adopt a multi-scale perspective for research and conservation, and consider the scale at which different organisms utilise their habitat. This is particularly important in floodplain landscapes, where fluvial processes and biotic factors maintain a heterogeneous micro-landscape, including a diverse mosaic of vegetation patches at different successional stages (Ward *et al.*, 1999; Ballinger *et al.*, 2007). The critical role of habitat heterogeneity at these scales has been demonstrated within this study, with staphylinid beetle assemblages responding to certain environmental gradients at microhabitat scales. While the scale to which different taxa react to habitat

heterogeneity may vary (Tews *et al.*, 2004), the positive effects of microhabitat heterogeneity on one of the most dominant taxa of the wetland ground fauna is likely to cascade up the food chain. With the increasing recognition of the need to conserve floodplain habitats (Maddock, 2008), small-scale studies are needed to understand the complex multi-scale relationships and provide the reference conditions for conservation and restoration practices. Within conservation programmes, the maintenance and facilitation of small-scale heterogeneity should be adopted as a priority at scales of tens of metres (Schaffers *et al.*, 2008).

The high diversity of microhabitats found in Alder Carr both in terms of vegetation and abiotic factors confirms that mature floodplain forests within Britain can still provide a mosaic of habitats across environmental and biotic spectra (Peterken & Hughes, 1995; Antvogel & Bonn, 2001; Hughes *et al.*, 2001; Apigian *et al.*, 2006; Barton *et al.*, 2009). However, as there was no significant relation to defined microhabitat categories within this study, heterogeneity at this scale may not be obvious to the human eye. Forest specialist species (as defined in the literature) were found in high abundances in heavily shaded plots, and a detritivorous species was found to be indicative of plots with high quantities of dead wood, highlighting the mosaic effect of these structurally complex floodplain forest habitats. Within increasingly homogenous agricultural landscapes, floodplain forests can add heterogeneity at both landscape and local scales and provide important habitat across the organismic spectrum (Peterken & Hughes, 1995).

While it is recognised that floodplain forests can provide heterogeneous habitat, the restoration of these habitats is still challenging due to limited extent, intensive surrounding land use and loss of species already associated with this environment (Peterken & Hughes, 1998). Peterken and Hughes (1995) suggest four options for floodplain forest restoration (Table 5.9). By reinstating natural flood disturbance regimes (options C and D), small-scale heterogeneity is promoted naturally, which can encourage a diversity of habitats. However, option D is an idealised option with limited application in its pure form (Peterken & Hughes, 1995), and where not possible, active promotion of small-scale heterogeneity within floodplain forests should be pursued. Restoration of within river heterogeneity has been addressed in the past couple of decades, for example the Environment Agency uses riffle replacement, current deflectors and artificial reef creation as tools in everyday fisheries (Harper *et al.*, 1999). Additionally, the felling of trees into rivers to serve as large woody debris has been adopted to enhance channel morphology, flow variations, microhabitat diversity, and

ultimately density and diversity of macro-invertebrates (Gerhard & Reich, 2000). Equivalent practices like these on floodplains, including the felling of a select few trees for the promotion of dead wood areas, could be performed to enhance the heterogeneity of floodplain forest habitats.

Table 5.9 Options for floodplain forest restoration as outlined by Peterken and Hughes (1995). Options A-D represent the extremes between which intermediate alternatives are possible.

		Forest	
		Managed	***Not Managed***
River	***Managed***	**A:** Plant woodland on a floodplain whose river remains constrained within existing channels	**B:** Establish new native woodland, but leave it to develop naturally. The river remains constrained within existing channels
	Not Managed	**C:** Plant new woodland on a floodplain where the river is allowed to flood and meander without restraint	**D:** Establish new native woodland, but leave it to develop naturally on a floodplain where the river is allowed to flood and meander without restraint

Finally, as emphasised throughout this thesis, research into the diversity of staphylinid beetles is limited in any landscape, largely due to the sheer numbers of species and difficulty associated with their identification (Hammond, 1998; Lott, 2009; Lott & Anderson, 2011). While no causal links can be confirmed between vegetation cover and composition and staphylinid diversity at this scale, a developed understanding of these links could prove fundamental in the conservation and restoration of British floodplain forests. Targets in terms of 'extent' and favourable status have been outlined nationally (UK Biodiversity Group, 1998) and at a county scale (e.g. Norfolk Biodiversity Partnership, 2004), but like many riverine restoration projects, little has been defined for their evaluation (Kondolf & Micheli, 1995). Vegetation is most commonly used to develop guidelines for conservation due to ease and speed of sampling and knowledge of species and communities. Using vegetation as a general indicator for the composition of other taxa is a widespread approach (Myers *et al.*, 2000; Xu *et al.*, 2008), primarily because the long-term monitoring of large numbers of species needed to detect changes in diversity especially of mega-diverse taxa is beyond the resources available to most ecological and environmental monitoring and conservation networks (Scott & Anderson, 2003). However, evaluation of floodplain forests on the basis of vegetation alone could underestimate the conservation value of invertebrate-rich but

botanically unexceptional areas within these forests. For example, bare ground is void of plant species but has been identified as an important habitat for beetles and other invertebrates (Key, 2000), and within Alder Carr provided habitat for a disguisable assemblage of beetles (Understorey Woodland microhabitat). If a more detailed relationship between vegetation and beetles were to be investigated at this scale, and if vegetation composition, the presence of specific plant species, vegetation cover, or lack thereof can be indicative of staphylinid beetle diversity, carabid beetle diversity and potentially other taxonomic diversity, conservation goals can be set effectively, evaluated efficiently and enable the incorporation of a number of taxonomic groups.

5.5 Conclusion

Species found in the River Wissey Alder Carr habitats represented only a small subset of carabid and staphylinid species associated with this habitat type (Luff, 1998; Lott, 2003), a number of which are scarce and threatened (Hyman & Parsons, 1992) and would therefore not be expected in the limited areas of floodplain forests remaining in Britain today (Hammond, 1998). While of a relatively mature age, chalk river floodplain forests like Alder Carr still do not represent old mature woodlands that once dominated floodplains in Britain (Peterken & Hughes, 1995; Peterken & Hughes, 1998), which are associated with a specific set of species linked with larger areas of old growth forests (Gibb & Cunningham, 2010). Rare and endangered stenotopic hygrophilous species are more likely found in natural and untouched stands of floodplain forests in central Europe (Bonn *et al.*, 2002).

Despite the lack of iconic and notably rare species and unclear distribution of staphylinid species within microhabitat categories, by using a microhabitat scale approach to investigate the beetle communities of these floodplain forests, this study has highlighted the small-scale heterogeneity still supported by these environments. Increasingly rare habitats in British riverscapes, this research has reiterated the importance of remnant floodplain forests, which should not be overlooked in floodplain conservation or restoration practices. In particular for maintaining and enhancing biodiversity in floodplain forests, restoration practices as outlined by the UK Biodiversity Action Plan (Maddock, 2008) need to consider heterogeneity of micro-topography, flood disturbance regimes, canopy, litter, age amount of dead wood within practical work and evaluation criteria.

Chapter 6. Functional trait diversity of beetle communities on chalk floodplain habitats

6.1 Introduction

In anthropogenically-altered environments, it is critical to understand the mechanisms underpinning relationships between habitat change, landscape complexity and biological diversity in order to suitably inform management and conservation practices (Lambeets *et al.*, 2009). The assessment of taxonomic α- and β-diversity provides information about species declines and changes in community composition, and can illustrate individual and community responses to anthropogenic disturbances. However, it has been suggested that communities are poorly described by species lists alone. A better understanding of composition, biotic interactions and responses to environmental gradients can be achieved if species and assemblages are classified according to their functional traits (Whittaker, 1975; Cole *et al.*, 2002). The ability to explain and predict patterns of species richness and composition relies on species showing different responses to environmental gradients and occupying different niches (Cadotte, 2011). Species vary in the activities or functions they perform within a habitat, investing in different tactics to optimise fitness and ensure their survival (Southwood, 1988). Therefore approaches that integrate these biological differences amongst species might more fully reveal the connections between environmental fluctuations, species occurrences and community process (Gerisch *et al.*, 2012). Floodplain habitats host specialised and vulnerable fauna adapted to the unique terrestrial-aquatic interface, disturbance regimes and resultant environmental heterogeneity (Andersen & Hanssen, 2005; Sabo *et al.*, 2005). A full understanding of the spectrum of biodiversity is crucial to inform the conservation of these heavily impacted yet fragile floodplain ecosystems.

Species traits are well-defined and measurable properties of an organism, primarily morphological and ecological characteristics, that allow them to survive in their environments (McGill *et al.*, 2006; Gerisch, 2011). 'Function' has been widely used in

conjunction with species traits due to the association of traits with the different functions that species perform. Thus functional traits have been further defined as a trait that strongly influences organismal performance (McGill *et al.*, 2006). Morphological traits reflect the way in which species physically interact with their environment, by facilitating or constraining organisms to perform specific tasks (Barton *et al.*, 2011a). Ecological traits, also referred to as life-history traits, are specific tasks or behaviours that species carry out, for example feeding and breeding habits. Habitat affinity, as the degree of association of a species with a specific habitat or microhabitat, can be considered within the context of functional traits because it recognises specialisation and habitat niches. The extent to which combinations of these traits differ between species coexisting in a community is a measure of trait diversity (Weiher, 2011). Although species traits are inherently linked to their phylogeny, the response of species to biotic and abiotic disturbances can vary substantially due to differences in the explicit expressions of their functional traits (Ewers & Didham, 2006; Clough *et al.*, 2007; Bettacchioli *et al.*, 2012). Therefore, classification of the relationship between habitat characteristics and the range of functional traits of species occupying these habitats may enable more robust understandings of the forces behind assemblage composition and therefore enhance predictive capabilities in constantly changing environments (Ribera *et al.*, 2001).

The habitat templet theory (Southwood, 1977, 1988) aims to construct a predictive framework for relationships between species traits and environmental and anthropogenic influences. The theory assumes that a habitat provides the templet upon which species' morphological traits evolve, but also upon which the ecological sorting of species that occupy the respective habitat occurs (Ribera et al 2001). Accordingly, any alterations to this habitat could be expected to alter the templet for certain species traits (Resh *et al.*, 1994).

In relation to the habitat templet theory, this chapter will focus on the functional diversity of carabid and staphylinid beetle communities in floodplain environments, and assess the influence of anthropogenic and environmental variables on species' traits. Recently, there has been increasing research into the response of carabid beetle community traits to human disturbance and land use change. Not only has there been a shift in communities towards increasing dominance of habitat generalist populations with decreasing numbers of specialists (Kotze & O'Hara, 2003; Barbaro & Van Halder, 2009; Bettacchioli *et al.*, 2012), but recent studies have also linked key morphological and ecological traits to sensitivity and declines in certain species and their populations.

Declines in large carabid beetles have been linked to both loss of habitat and habitat fragmentation (Kotze & O'Hara, 2003; Brooks *et al.*, 2012), related to the lower productive output and lower dispersal powers characteristic of these large species (Kotze & O'Hara, 2003; Gobbi & Fontaneto, 2008). Other studies have linked breeding and adult activity periods (Barbaro & Van Halder, 2009), differences in dispersal ability (Bettacchioli *et al.*, 2012) and feeding habits (Purtauf *et al.*, 2005) to sensitivity to anthropogenic land use change.

Similar to the other topics addressed in this thesis, there has to date been very limited research linking staphylinid community traits to differing habitats or habitat change. Studies of this nature have lagged behind carabids partly due to the reputation of staphylinids as being hard to identify (Lott, 2009; Lott & Anderson, 2011), but also due to limited information and ecological knowledge of staphylinid species' functional traits and habitat affinities. However, from a functional perspective, the importance of staphylinid beetles must be emphasised, as they are not only represented across the feeding spectrum as detritivores, herbivores, fungivores and predators (Clough *et al.*, 2007), but are one of the most ecologically important insect components of the soil fauna (Bohac, 1999) and the most dominant in pitfall trap catches across the studied floodplain habitats.

There is an overall need for multi-taxa, multi-scale approaches in functional diversity studies (Griffiths *et al.*, 2007; Barbaro & Van Halder, 2009) to assess at what scales anthropogenic drivers influence assemblage structure and whether these changes are mirrored across multiple taxa. To generate more robust causative links between anthropogenic drivers and the distribution of carabid and staphylinid assemblages within chalk floodplain landscapes, a functional perspective was adopted in this chapter at both macrohabitat and microhabitat scales, taking the following questions into consideration: (1) How does functional diversity vary at macrohabitat and microhabitat scales? (2) Which functional traits of beetle assemblages differentiate between the floodplain habitats and their management regimes? (3) What are the dominant anthropogenic and environmental factors influencing beetle traits in these habitats at landscape, site and microhabitat scales? (4) Are there parallels in the variation of trait compositions between carabid and staphylinid beetles? (5) To what degree do the taxonomical and trait-based classifications of beetle assemblage in floodplains show similarities?

6.2 Methodology

6.2.1 Field methods

In order to establish the trait diversity of beetles within floodplain habitats, a multi-scale approach was used, addressing both the macrohabitat scale represented by sampling 15 floodplain sites along three chalk rivers in Norfolk, UK, and the microhabitat scale represented by the more intensive short-time survey of a single floodplain woodland on the River Wissey, Norfolk (Table 6.1). Full site descriptions are given in Chapter 2, and the sampling of beetles at the macrohabitat and microhabitat scale has already been outlined in Chapter 3 and Chapter 5, respectively. At both scales relevant landscape, site and microhabitat variables were categorised as used in Chapters 3-5 (Table 6.2).

Table 6.1 Macrohabitat site names, abbreviations and habitat types, and microhabitat types and abbreviations.

Scale	Site/Plot Name	Code	Habitat	River	No. Plots
Macrohabitat scale	Hunworth Castle	HCA	Meadow	Glaven	5
	Hunworth Railway	HR	Meadow	Glaven	5
	Hunworth Meadow	HM	Meadow	Glaven	5
	Moorgate Meadow	MM	Meadow	Bure	5
	Ingworth Bridge	IB	Meadow	Bure	5
	Holt Lowes Fen	HLF	Fen	Glaven	5
	Glaven Farm	GF	Fen	Glaven	5
	Wildflower Fen	WF	Fen	Glaven	5
	Holt Lowes Woodland	HLW	Woodland	Glaven	5
	Hunworth Woods	HW	Woodland	Glaven	5
	Wildflower Woods	WW	Woodland	Glaven	5
	Mill Carr	MC	Woodland	Bure	5
	Shepherd's Carr	SC	Woodland	Bure	5
	Rough Pasture Carr	RPC	Woodland	Bure	5
	Alder Carr	AC	Woodland	Wissey	5
				Total	***75***
Microhabitat scale	Understorey Woodland	UW	Woodland	Wissey	9
	Dead Wood	DW	Woodland	Wissey	8
	Nettle- and Redcurrant-dominated	RN	Woodland	Wissey	8
	Tussock Grass-dominated	TG	Woodland	Wissey	7
	Iris- and rush-dominated	IR	Woodland	Wissey	7
	Wooded *Phragmites*	WP	Woodland	Wissey	6
				Total	***45***

Table 6.2 Characterisation of macrohabitat site and landscape variables, and microhabitat environment variables

Scale		Variable
Macrohabitat scale	Site descriptors	Habitat Type
		Site Area (m^2)
		Vegetation Composition (%)
		Vegetation Cover (%)
		Grazing
		Cutting
	Landscape descriptors	River
		Perimeter (m)
		Edge Density (ED)
		Landscape Pattern Index (D_1)
		Surrounding Arable Land (SA) (%)
		Surrounding Woodland (SW) (%)
		Surrounding Meadow (SM) (%)
Microhabitat scale	Vegetation	Plant species (%)
		Average plant height (m)
		Plant Cover (%)
		Moss cover (%)
		Twig cover (%)
		Dead wood cover (%)
		Litter cover (%)
	Soil characteristics	pH
		Moisture (%)
		Organic content (%)
	Microclimate	Light intensity (lux)

6.2.2 Beetle functional traits

The selection of traits for ecological studies is of fundamental importance because all subsequent classifications and calculations of ecological similarity are dependent on them (Weithoff, 2003). Here, four morphological, three ecological and two habitat association traits of carabid species were chosen (Table 6.3), based on their suggested ability to provide information on and predictions for species sensitivity to human disturbance and landscape fragmentation (Ribera *et al.*, 1999; Ribera *et al.*, 2001; Barbaro & Van Halder, 2009; Barton *et al.*, 2011a). Due to the limited literature available on staphylinid species, only four traits categories were obtainable for the members of this family (Table 6.3).

After the sorting and identification of beetles, morphological and ecological traits were obtained for all species from a wide range of literature sources (Hinton & Stephens,

1941; Frank, 1968; Kasule, 1968; Nield, 1976; Thiele, 1977; Dennis, 1989; Grafius & Warner, 1989; Buse & Good, 1993; Dennis & Sotherton, 1994; Anderson, 1997; Glesne, 1998; Luff, 1998; Betz, 1999; Ribera *et al.*, 2001; Lott, 2003; Boháč *et al.*, 2007; Clough *et al.*, 2007; Honek *et al.*, 2007; Luff, 2007; Lott, 2009; Sobek *et al.*, 2009; Loubère, 2010; Lott & Anderson, 2011; Watford Coleoptera Group, 2011).

Beetle size was determined by taking an average of the maximum and minimum sizes for each species in the literature. Size categories were then defined by ranking these average sizes for carabid and staphylinid beetle species separately, and dividing each list into four categories of approximately equal numbers of species. Body colour was categorised into dark, metallic and pale according to both collected adult samples and the relevant literature (Luff, 1998; Luff, 2007). Wing development was divided into three categories: brachypterous, dimorphic and macropterous. Brachypterous species, which have short wings, and fully apterous species without wings, were both classified as brachypterous, as it is assumed that their flight ability is generally extremely limited. Macropterous species are those with only long wings, while dimorphic species are those where both long and short winged individuals have been recorded. It is assumed that flight and therefore dispersal capabilities is a function of carabid wing form. It must however be noted that even fully winged species do not necessarily have flight ability, as flight muscles may not be functional (Lindroth, 1974). Pronotum shape was also divided into three categories: oval, trapezoidal and cordiform (examples of which are shown in Figure 6.1). Feeding habitats were defined according to a species' principal food source. For staphylinids however, a number of species were categorised as omnivorous due to their wide-ranging diets. Breeding season for carabid species were primarily obtainable from Luff (2007). In cases where breeding season information was not outlined, inferences were made using their overwintering stages. If a species overwinters as larvae, they are assumed to breed in autumn, and if they overwinter as adults, they breed in spring (Steel, 1970). Habitat affinity was defined using the broad selection of literature outlined above. When no mention of canopy or moisture preferences was identified, an informed prediction was made depending on the suggested habitat preferences; for example, 'waters edge' suggests wet affinity. When inconsistencies in the literature arose, the most local to the study area and most recent references were used (Lott, 2003; Luff, 2007; Lott, 2009; Lott & Anderson, 2011). Where multiple and contrasting canopy and moisture affinities were suggested, species were categorised into 'No Preference'. A full table of species and their associated traits is given in Appendix 8.

Table 6.3 Beetle functional traits recorded for carabid (C) and staphylinid (S) beetles.

Trait Type	Trait	Trait Categories	C	S
Morphology	Body size	Taken in mm but also categorised into the following: Carabid: very small <=4 mm, small 4.1-8 mm, medium 8.1-14 mm, large 14.1 mm+ Staphylinid: very small <=4 mm, small 4.1-6 mm, medium 6.1-9 mm, large 9.1 mm+	•	•
	Body colour	Dark, metallic, pale	•	
	Pronotum shape	Cordiform, oval, trapezoidal	•	
	Wing development	Brachypterous (or apterous), dimorphic, macropterous	•	
Ecology	Breeding season	Spring, summer, autumn and winter	•	
	Diel activity	Diurnal, nocturnal, both	•	
	Feeding habits	Carabids: predator, herbivore Staphylinids: detritivore, fungivore, herbivore, omnivore, predator	•	•
Habitat Affinity	Canopy preference	Open, closed, no preference	•	•
	Moisture preference	Dry, wet, no preference	•	•

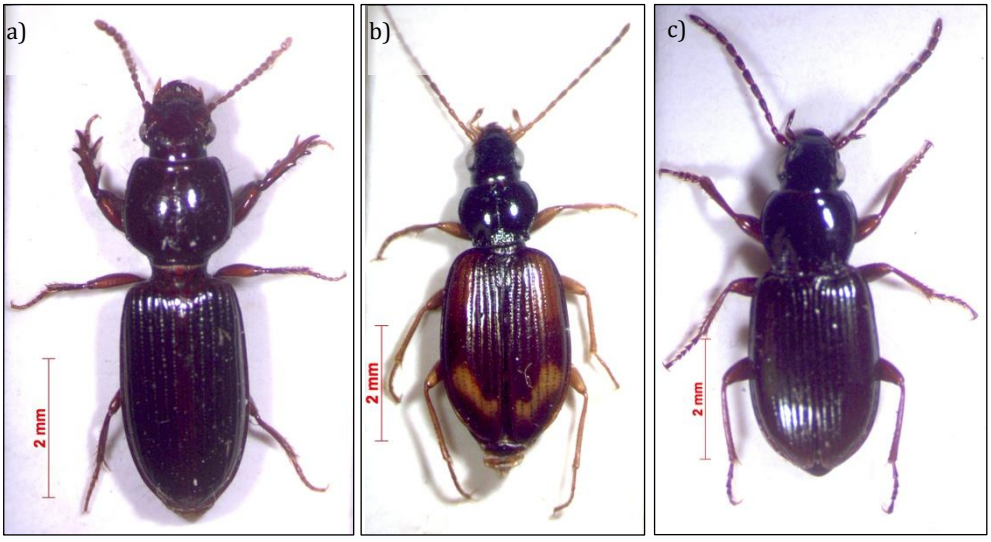


Figure 6.1 Difference in pronotum shape between three carabid beetles: a) Clivina fossor *with oval-shaped pronotum, b)* Bembidion tetracolum *with cordiform- (heart) shaped pronotum, and c)* Pterostichus diligens *with trapezoidal pronotum.*

6.2.3 Statistical analysis

Relationship between functional traits and habitat type

To determine the differences in the occurrence of particular species' traits between habitat types, one-way analysis of variance (ANOVA) and Tukey's HSD *post hoc* tests were performed using the community-weighted matrix (CWM) of species traits for each site and habitat as the explanatory variable. The CWM represents the relative proportion of each trait category present in each measurement unit (plot or site), by weighting traits according to abundances of species possessing those traits. These calculations were conducted using the 'FD' package in R (Laliberté & Shipley, 2011; R Development Core Team, 2011).

Functional diversity indices

A number of metrics were used to establish the functional diversity of carabid and staphylinid communities within the macrohabitat and microhabitat landscapes. The division of functional diversity into different components, namely richness, evenness and divergence, has been shown to provide a more suitable method for its quantification rather than using single functional diversity indices (Mason *et al.*, 2005; Villéger *et al.*, 2008; Mouchet *et al.*, 2010).

Functional richness which represents the range of traits within a multidimensional space (Gerisch *et al.*, 2012) was calculated using the multidimensional index of Villéger *et al.* (2008). This richness index (F_{Ric}), also known as the convex hull volume, is a measure of the functional space filled by a community. Higher values of functional richness represent a more functionally diverse community (Gerisch *et al.*, 2012). In addition, a measure of functional dispersion (F_{Dis}) was calculated. This also analyses the functional space filled by a community, but is calculated as the abundance-weighted mean functional distance to the common centroid of all species (Laliberté & Legendre, 2010). A measure of functional evenness (F_{Eve}) was calculated in order to measure how evenly trait abundances are distributed in multidimensional trait space (Villéger *et al.*, 2008; Gerisch *et al.*, 2012). Measures of evenness indicate the level of effective utilisation of resources available to a community, where a low F_{Eve} indicates that some parts of the niche space may be under-utilised (Mason *et al.*, 2005). Finally, a measure of the spread of abundance within the functional trait space occupied by a community (F_{Div}) was assessed (Mason *et al.*, 2005; Villéger *et al.*, 2008). The respective value, $F_{Div,}$ is similar to F_{Dis}, but measures the distances of only the most abundant species to the central point in multidimensional trait space, and indicating the degree

of spread in functional traits and therefore niche differentiation and resource competition within the assemblage (Mason *et al.*, 2005).

To calculate these indices (F_{Ric}, F_{Dis}, F_{Eve} and F_{Div}), a square-root corrected Gower dissimilarity index was computed, which allows for the measurement of dissimilarity for mixed variables such as trait categories (Gower, 1971; Podani, 1999). At a macrohabitat scale, measurements were calculated for each site and at a microhabitat scale, for each plot. All of these analyses were performed using the 'FD' package in R (Laliberté & Shipley, 2011; R Development Core Team, 2011).

To establish whether any relationships existed between the trait diversity measurements and landscape, site and microhabitat variables, Pearson's Product-Moment Correlations were computed. Prior to the analysis, variables were tested for normal distributions using Shapiro-Wilk tests and QQ-plots and were transformed accordingly where required.

Factors influencing functional diversity of beetle communities

To further assess the influence of landscape, site and microhabitat variables on the functional traits of beetle communities, a redundancy analysis (RDA) was performed on each CWM and the transformed explanatory variables. To include vegetation community composition as an explanatory variable, a Principal Component Analysis (PCA) was performed on arc-sine transformed plant species data. Using the scree plot method, the first two PCs were identified as 'interpretable' and included as variables in the RDA. As trait abundances were proportional, they were also arc-sine transformed prior to analysis. To select the most suitable variables for the model, an inclusive forward selection procedure using Akaike's Information Criterion (AIC) was performed on the landscape, site and microhabitat data, separately, to identify those factors explaining the most variance in carabid and staphylinid trait assemblages. AIC provides a measure of high constrained inertia, but penalises for the number of chosen parameters (Bozdogan, 1987; Oksanen, 2011). Multi-collinearity was accounted for by ensuring that correlated variables such as area, perimeter and edge density were not incorporated together in the final model. If the variables showed significant correlations, the variable explaining the most variance in the dependent factor was chosen in place of the others. Hill's N_2 diversity function, which is the inverse of Simpson's D (Hill, 1973), was used to present ordinations by giving graphical plotting priority to sampling plots and traits associated with higher abundances.

In addition, variance partitioning analysis (pRDA) was performed on each CWM to analyse the relative importance of landscape, site and microhabitat factors in structuring the trait composition of communities. pRDA partitions the total percentage of variation explained by an RDA into unique and common contributions for the specified predictor variables (Borcard *et al.*, 1992). The most significant models identified in the RDA were used as predictors in the respective macrohabitat and microhabitat pRDAs. The spatial distribution of plots was also used at both scales to establish whether any biogeographical influences could be recognised. Spatial variables were constructed using a Euclidean distance matrix of the XY coordinates of each plot. Principal coordinate analysis (PCoA) was then performed on the matrix and the positive eigenvalues of the PCoA were used as a set of spatial predictors for each pRDA. The significance of each fraction of the pRDA was tested using 9999 permutations. Both RDA and pRDA analyses were carried out using the 'ape' and 'vegan' packages in R (De Cáceres & Legendre, 2009; R Development Core Team, 2011).

Relationship between assemblages: taxonomy versus traits and carabid versus staphylinid beetles

The use of RDA and pRDA within this chapter enabled comparability with previous analysis regarding the influence of landscape, site and microhabitat variables on carabid and staphylinid communities as defined by their species composition (the focus of Chapters 3 and 4). To further investigate links between species diversity and functional diversity, two analytical methods were used here. Firstly, Pearson correlation coefficients were computed on each functional trait diversity index (F_{Ric}, F_{Dis}, F_{Eve} and F_{Div}) in relation to three species-diversity indices calculated in Chapter 3 (Shannon Weaver, Simpson's D and Fisher's-α, equations in Table 3.5). Secondly, to further determine the degree to which the occurrences of species and the occurrences of species traits were correlated, Procrustes rotation analysis was performed. This method aims to find the maximum similarity in data points between two ordination models by rotating and rescaling one ordination model towards a target ordination (Legendre & Legendre, 1998; Gerisch, 2011). Rather than using Mantel Tests, which evaluates correlation between two distance matrices, Procrustes rotation analysis uses raw data matrices and enables visualisation of the similarity between ordinations, and as such has been shown to be more suitable in the comparison of two multivariate data matrices (Peres-Neto & Jackson, 2001). Following the approach outlined by Gerisch (2011), two Procrustes rotations were performed for carabid and staphylinid data at each scale: i) rotation of a species-PCA model against a trait-PCA model (without

environmental variables) and ii) rotation of a species-RDA model against a trait-RDA model, both constrained by the full set of descriptor variables to estimate if anthropogenic and environmental variables affect the correlation.

To establish if any similarities existed between carabid and staphylinid assemblages according to their functional traits, a further Procrustes analysis was finally calculated. For this analysis, due to the different trait categories available for the two families as outlined in Table 6.3, CWMs were calculated based on the four trait categories available for both families, namely size, feeding guild, canopy preference and moisture preference. These analyses was performed using the 'vegan' package (Oksanen *et al.*, 2012) in R (R Development Core Team, 2011).

6.3 Results

Across the 15 floodplain sites at a macrohabitat scale, 3129 carabid beetles and 4931 staphylinid beetles were collected and identified to one of 53 and 89 species respectively. Within Alder Carr specifically for the fine-detailed microhabitat sampling, a total of 244 carabid beetles and 1027 staphylinid beetles were collected over the two-week sampling period and identified to one of 22 and 42 species respectively. The low overall abundances of carabid beetles at the microhabitat scale precluded any comparison in traits composition, leaving macrohabitat carabid and staphylinid and microhabitat staphylinid assemblages available for functional trait analysis. Two species were removed from the data prior to analysis due to limited information in the literature about habitat associations and their representation by only one specimen each: *Blemus discus* (Carabidae) and *Erichsonius signaticornis* (Staphylinidae).

Relationship between functional traits and habitat type

Habitat type had a significant influence on certain carabid functional traits (Figure 6.2 a-i). In particular distinct trait characteristics were evident in woodland habitats in comparison to both fen and meadow habitats. Morphologically, medium sized beetles were found in relatively higher proportions in woodland habitats. Collectively, over 80% of woodland carabid assemblages were comprised of medium and large specimens, whereas small beetles showed significant relative preference to fen habitats, on average accounting for 50% of specimens in these assemblages. Additionally, pronotum shape was found to be significantly different between habitat types, with woodland habitats supporting significantly higher proportions of carabid

beetles with cordiform pronotum (average over 40%), and significantly lower proportions of specimens with oval-shaped pronotums (approximately 10%). Woodland habitats also supported the highest proportion of brachypterous carabid beetles, which made up a third of the assemblage, whereas brachypterous specimens only made up 3% on average of fen habitat assemblages. Ecologically, there were no significant differences between habitats for carabid specimens of different feeding guilds or in the percentage of nocturnally and diurnally active beetles. However, breeding season varied significantly between habitat types, as woodlands supported higher proportions of autumn and winter breeders (average 50%), whereas fen habitats hosted an average of almost 80% of spring breeders. Additionally carabid species showed significant differences in open and closed habitat affinity, with meadow habitats hosting significantly higher proportions of carabid beetles with specific association to open habitats (average 20%). Interestingly woodland habitats hosted the lowest proportion of characteristically closed habitat specimens. Carabid beetles with no recorded preference in the literature to open or closed canopy dominated all habitat types. Fen habitats hosted the highest proportion of wetland-specific specimens (almost 80%) and woodlands the lowest (40%). Habitat type did not significantly influence the analysed functional traits of staphylinid beetle assemblages (Figure 6.3). ANOVA and *post hoc* calculations identified a single significant comparison; woodland habitats hosted a significantly higher proportion of closed canopy specialists than meadow and fen habitats.

At a microhabitat scale, microhabitat type showed little influence on the functional traits of staphylinid assemblages (Figure 6.3). However, one significant observation was the preference of wetland specialists to Understorey Woodland and Wooded *Phragmites* plots, particularly in comparison to Dead Wood plots (Figure 6.4.d). In addition, very small species showed significant preference for Dead Wood habitats, whereas medium sized species showed preference to Tussock Grass and Wooded *Phragmites* habitats. Only two feeding guilds were used in this analysis as a single specimen only represented each category of herbivore, fungivore and omnivore feeding habits.

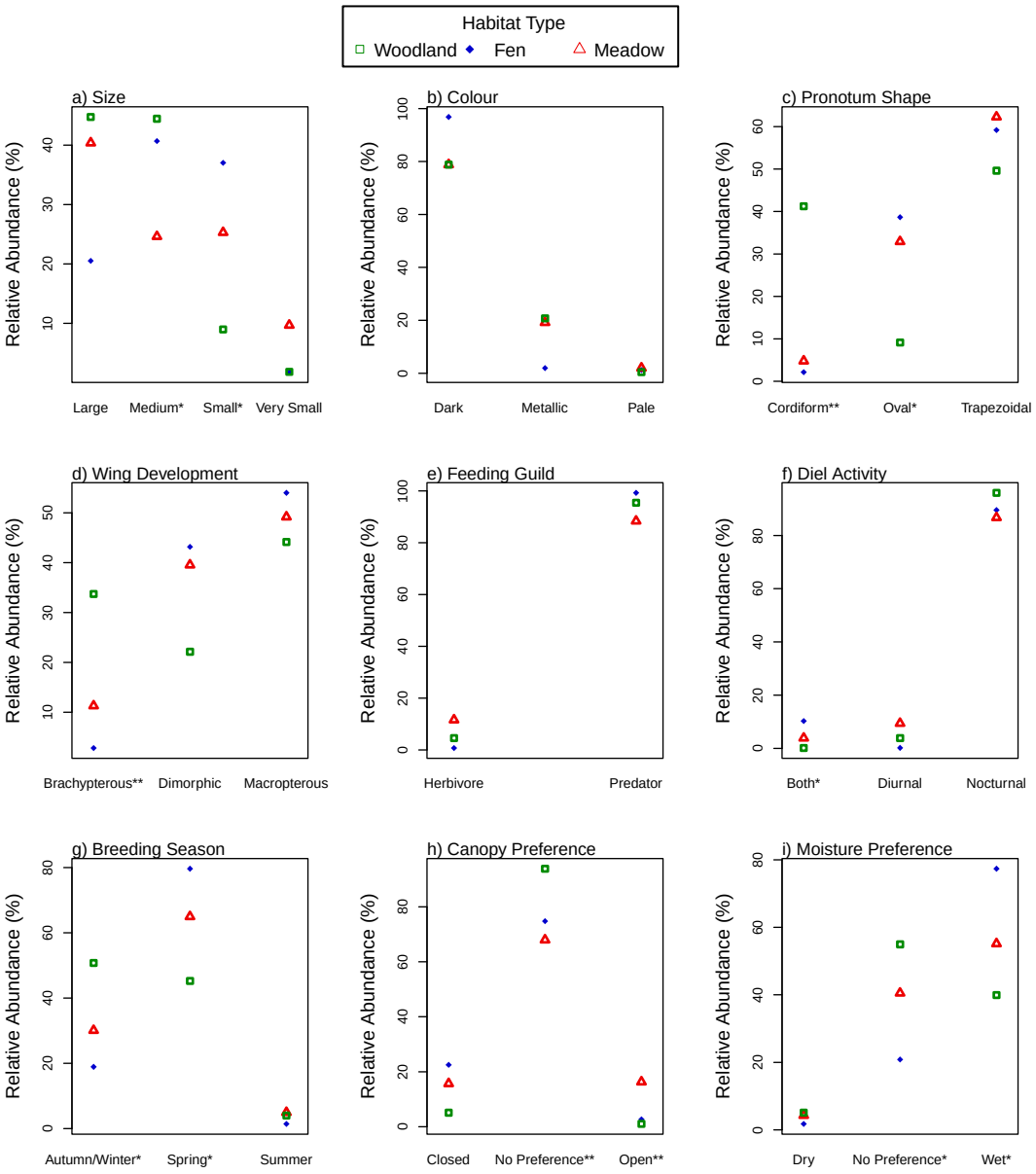


*Figure 6.2 Macrohabitat scale: mean proportion of carabid species traits for each habitat type. Significance for each ANOVA calculation are given as '**' <0.01, '*' <0.05.*

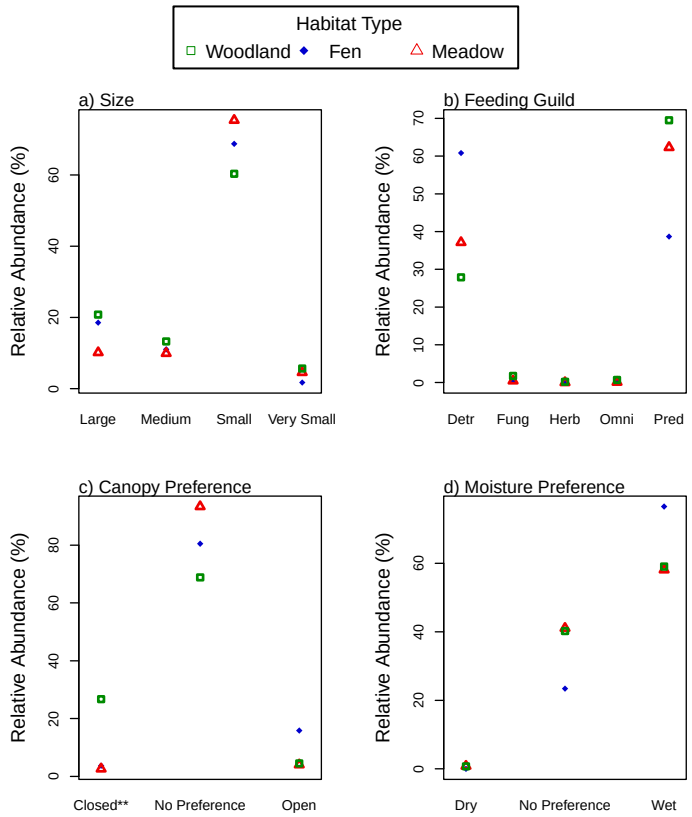


*Figure 6.3 Macrohabitat scale: mean proportion of staphylinid species traits for each habitat type. Feeding guilds are abbreviated as: Detr – Detritivore, Fung – Fungivore, Herb – Herbivore, Omni – Omnivore and Pred – Predator. Significance for each ANOVA calculation are given as '**' <0.01, '*' <0.05.*

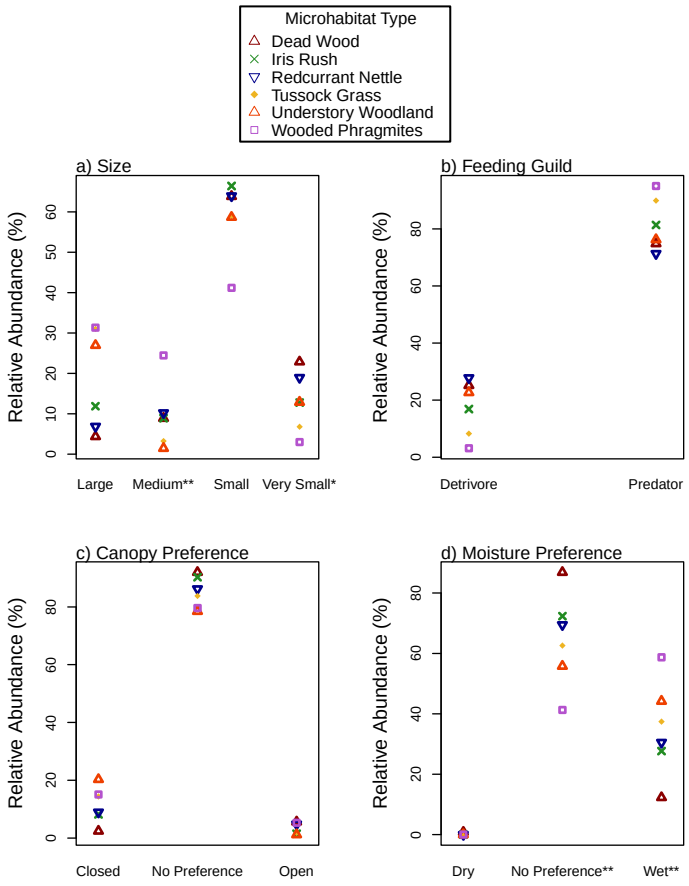


*Figure 6.4 Microhabitat scale: mean proportion of staphylinid species traits for each microhabitat type. Significance for each ANOVA calculation are given as '**' <0.01, '*' <0.05*

Functional diversity indices

There was a significant difference in both functional richness and functional dispersion for carabid beetles between habitat types (F_{Ric} $F_{2,12}$=5.51, p=0.02; F_{Dis} $F_{2,12}$= 9.62, p<0.01; Figure 6.5). Fen habitats displayed low functional richness and functional dispersion, but more even trait assemblages. In comparison, woodland and meadow habitats showed on average lower functional evenness, and woodland habitats presented the lowest function divergence values. In regards to staphylinid beetles, woodland habitats hosted functionally rich staphylinid assemblages, significantly more so than meadow and fen habitats (F_{Ric} $F_{2,12}$=18.48, p<0.01; Figure 6.6). There were no significant differences between habitats for other staphylinid functional diversity measures, although on average fen habitats had the highest functional evenness, and Holt Lowes Fen had the highest values for functional dispersion (F_{Dis}=0.311). Microhabitat scale functional diversity indices showed no significant differences between microhabitats (Figure 6.7).

Pearson's Product-Moment Correlations identified some significant, yet contrasting correlations between functional diversity indices and site and landscape factors across the macrohabitat and microhabitat scales. For carabid beetles, F_{Dis} was positively correlated with surrounding woodland (R=0.514, p<0.05), and F_{Eve} was positively correlated with edge density (R=0.583, p<0.05). For staphylinid functional diversity, F_{Ric} was negatively correlated with landscape complexity (D_1, R=-0.582, p<0.05) and F_{Dis} was negatively correlated with percentage of surrounding arable land (R=-0.611, p<-0.05). At a microhabitat scale, F_{Dis} was negatively correlated with light levels (R=-0.367, p<0.05) and F_{Eve} was negatively correlated with litter cover (R=-0.338, p<0.05).

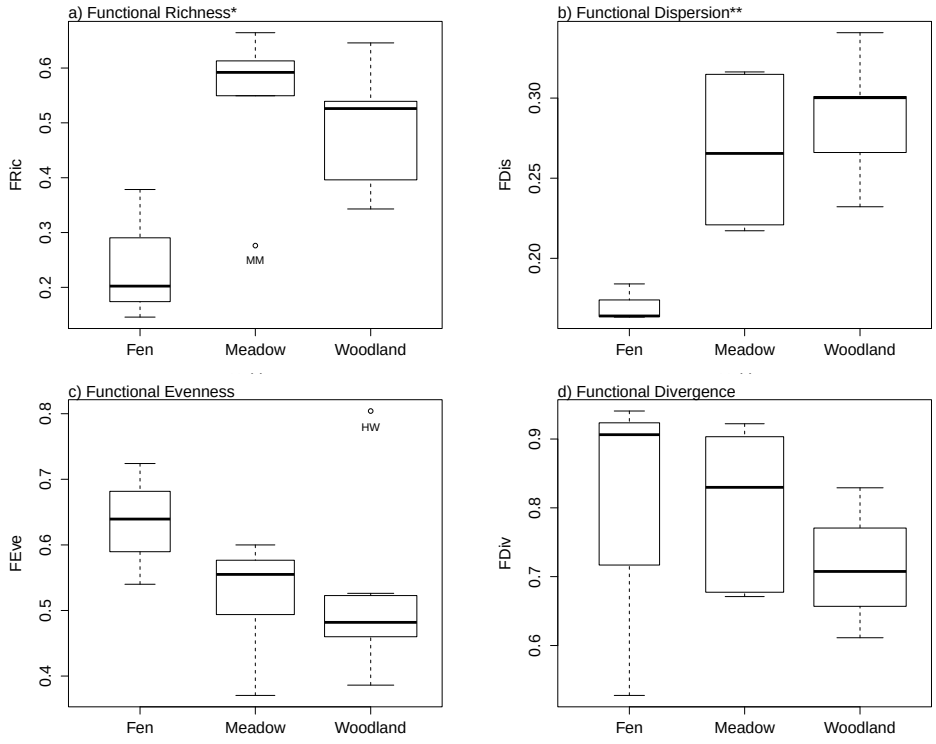


*Figure 6.5 Macrohabitat scale: carabid functional diversity indices compared by habitat type. Significance for each ANOVA calculation are given as '**' <0.01, '*' <0.05.*

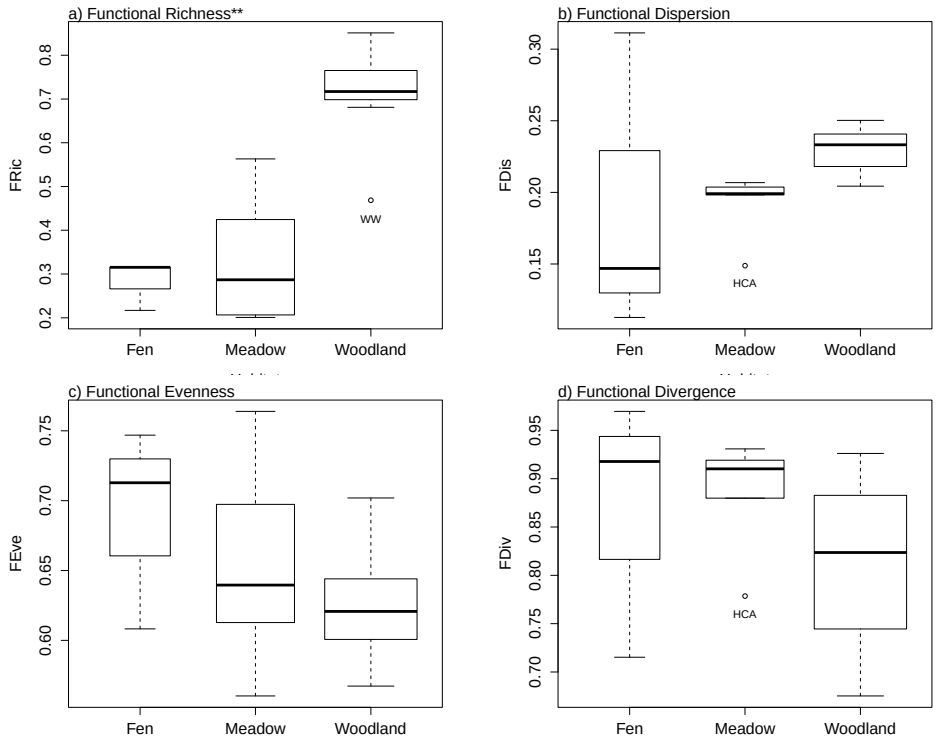


*Figure 6.6 Macrohabitat scale: staphylinid functional diversity indices compared by habitat type. Significance for each ANOVA calculation are given as '**' <0.01.*

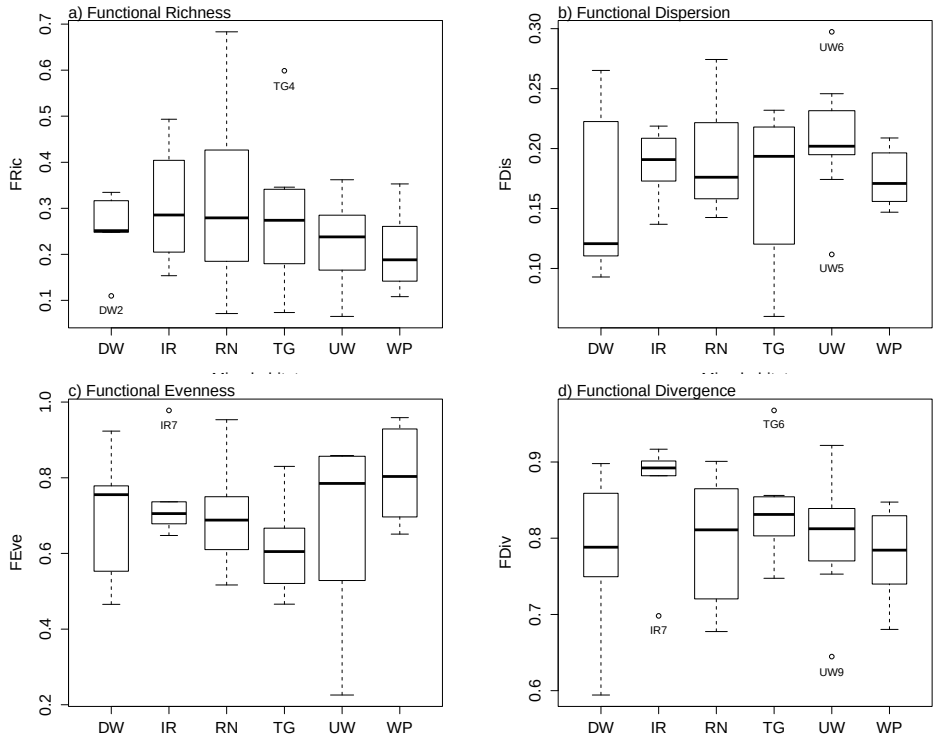


Figure 6.7 Microhabitat scale: staphylinid functional diversity indices compared by microhabitat type. No significance differences between microhabitats were identified in ANOVA calculations.

Factors influencing functional traits of beetle communities

RDA confirmed that the site factors, habitat type, grazing and area, were significant explanatory variables for both carabid and staphylinid trait composition at the macrohabitat scale (Table 6.4, Figure 6.8-6.9). Large, brachypterous, autumn and winter breeding carabids with cordiform pronotums were associated with woodland habitats with large areas, whereas wetland specialists and darker species were associated with fen habitats with limited areas (Figure 6.8). Small, diurnal, dimorphic carabids and those that are open habitat specialists showed preference to meadow habitats, and particularly dimorphic species were associated with meadow habitats experiencing a cutting regime. Spring breeders also showed preference to open fen and meadow habitats. For staphylinid beetles, large and medium size species were again associated with woodland habitats (Figure 6.9). Furthermore, area strongly affected the feeding guild of staphylinids, with the abundance of predatory species being associated with large sites and that of detritivorous species associated with small sites. Similarly to carabid species, wetland specialists were associated with small fen habitats.

Landscape pattern (D_1) had a significant influence on both carabid and staphylinid macrohabitat trait assemblages (Table 6.4, Figure 6.10-6.11). For carabids, macropterous species were associated with complex surrounding habitats, whereas large and predatory species were associated with reduced landscape complexity and high proportions of surrounding woodland. For staphylinids, large, closed canopy preferring species were associated with low surrounding landscape complexity, while small species were linked to high landscape complexity. Additionally, wet detritivorous staphylinid species were linked with high edge density values, while predatory species in comparisons were associated with low edge densities.

The influence of vegetation composition and richness on beetle functional traits was evident across both macrohabitat and microhabitat scales (Table 6.4). Vegetation composition was a significant factor explaining carabid macrohabitat trait assemblages, vegetation richness for staphylinid macrohabitat trait assemblages and vegetation composition at the microhabitat scale (Figure 6.12).

Variance partitioning confirmed the dominance of site scale factors on macrohabitat beetle trait communities (Figure 6.13-6.14). Site factors alone [S|L+SP] explained 23% and 19% of variance in carabid and staphylinid trait assemblages, respectively, in contrast to 2% for landscape factors alone for both families [L|S+SP]. Only the site

factor was significantly linked with staphylinid trait composition. Notably, the spatial distribution of plots [SP|S+L] explained 5% of variance in carabid trait assemblages. This suggests that, while the functional traits of carabid assemblages were influenced by an interacting combination of site, landscape and spatial factors, staphylinid species were chiefly influenced by site characteristics.

Microhabitat RDA analysis confirmed the lack of distinction between microhabitat types, identified by comparisons in individual traits and functional diversity indices. However, in addition to the significant influence of vegetation on assemblage traits at this spatial scale, the ordination suggested some association between detritivorous species and Dead Wood microhabitats (Figure 6.12). In the pRDA, the combination of significant abiotic, vegetation and spatial factors explained 23% of variance within staphylinid beetle assemblages. Abiotic factors alone [A|V+SP] explained 6% of variance. Vegetation [V|A+SP] explained the highest proportion of variance at 10%, and spatial distribution of plots [SP|A+V] explained 8%. This confirms an important influence of the vegetation composition at this spatial scale, but also suggests that spatial proximity has a significant influence on trait compositions within microhabitat assemblages.

*Table 6.4 Significant landscape, site and microhabitat variables for RDAs on carabid and staphylinid trait assemblages. Significance is shown as ** <0.01, * <0.05.*

Scale/Variables	Carabidae	Staphylinidae
Macro/Landscape	D_1 – Landscape Pattern**	Edge Density**
	Surrounding Woodland**	D_1 – Landscape Pattern**
Model	**AIC = 37.84, F=3.22, p<0.01**	**AIC=19.74, F= 6.17, p<0.01**
Macro/Site	Habitat**	Habitat**
	Area**	Area**
	Grazing**	Grazing**
	Cutting**	Cutting**
	Vegetation Composition (VegPC2)*	Vegetation Composition (VegPC2)*
Model	**AIC=19.74, F=6.17, p<0.01**	**AIC=19.74, F=6.17, p<0.01**
Micro/Microhabitat		Vegetation Composition (VegPC1)**
		Dead Wood*
Model		**AIC= -22.89, F=4.38, p<0.01**

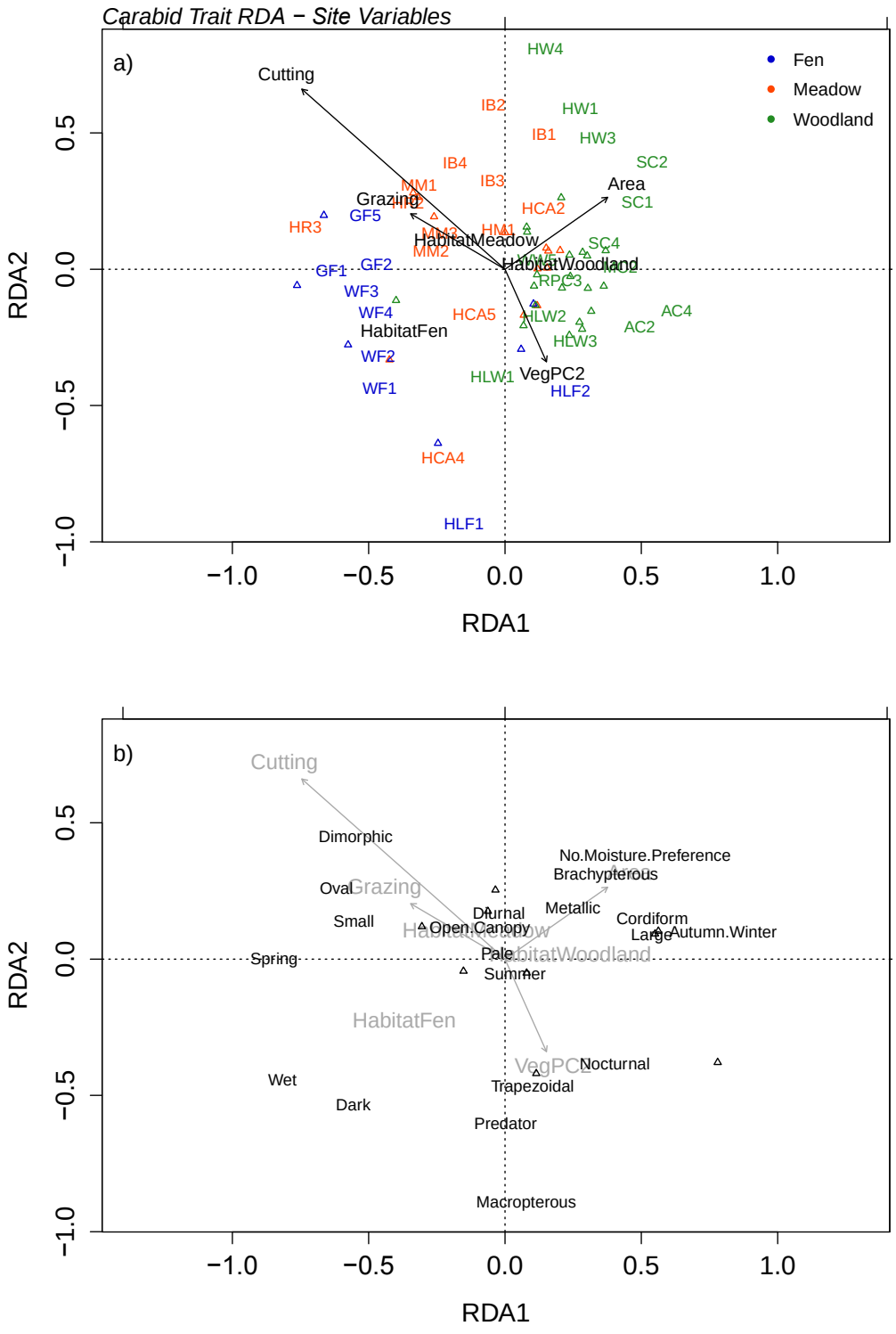


Figure 6.8 Redundancy analysis (RDA) of carabid assemblages at the macrohabitat scale according to functional traits and in relation to site variables. Plots in a) are labelled according to their site name and colours represent the different habitat types. Arrows represent significant site variables: Grazing, Cutting and VegPC2 (vegetation composition). Habitat labels, HabitatFen, HabitatMeadow and HabitatWoodland, represent the centroids of the factor-variable habitat. Traits are labelled in b). Labelling priority is given to those traits that are most abundant using the inverse of Simpson's diversity index. Those traits not labelled are marked as an open triangle.

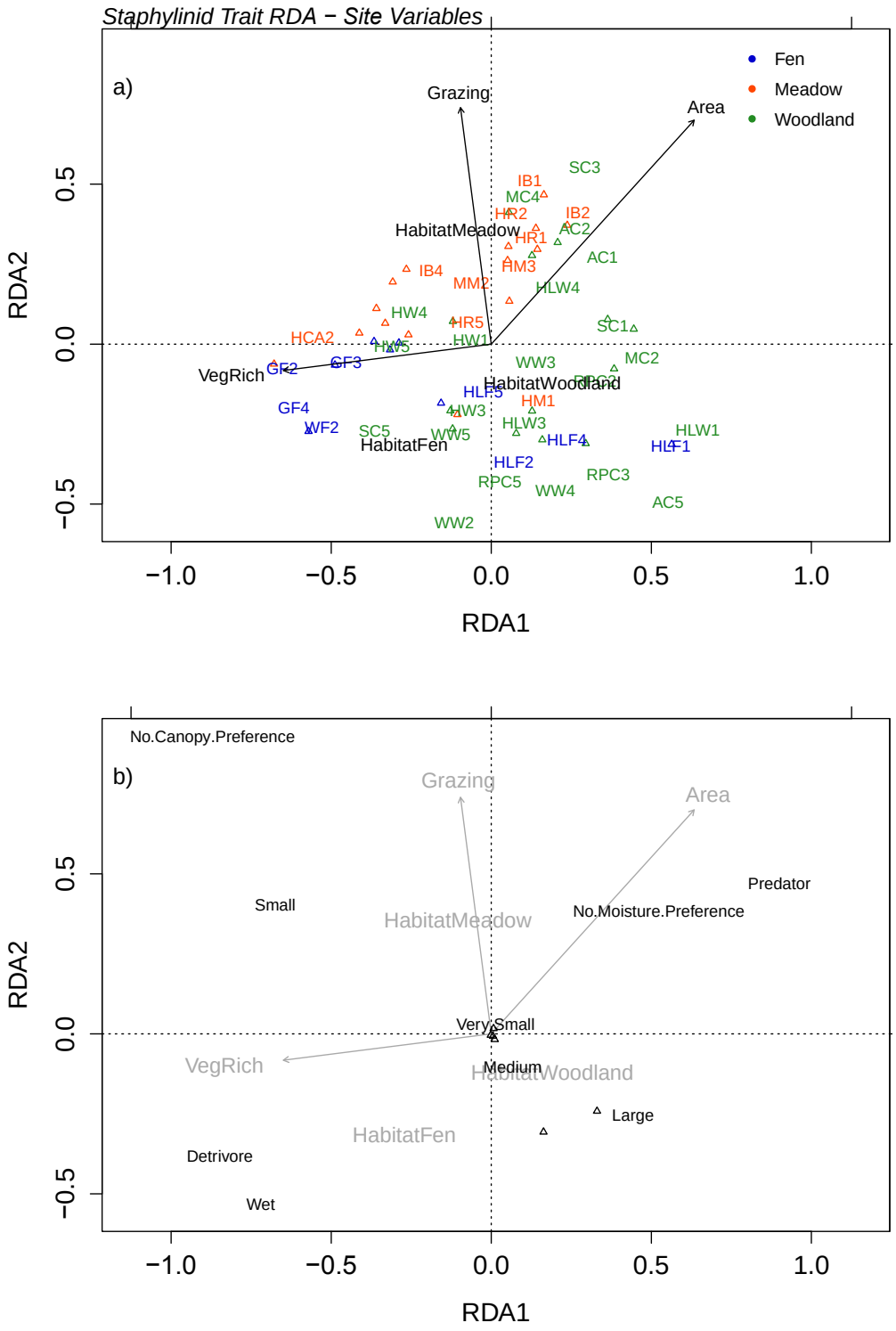


Figure 6.9 Redundancy analysis (RDA) of staphylinid assemblages at the macrohabitat scale according to functional traits and in relation to site variables. Plots in a) are labelled according to their site name and colours represent the different habitat types. Arrows represent significant site variables: Grazing, Area and VegRich (vegetation species richness). Habitat labels, HabitatFen, HabitatMeadow and HabitatWoodland, represent the centroids of the factor-variable habitat. Traits are labelled in b). Labelling priority is given to those traits that are most abundant using the inverse of Simpson's diversity index. Those traits not labelled are marked as an open triangle.

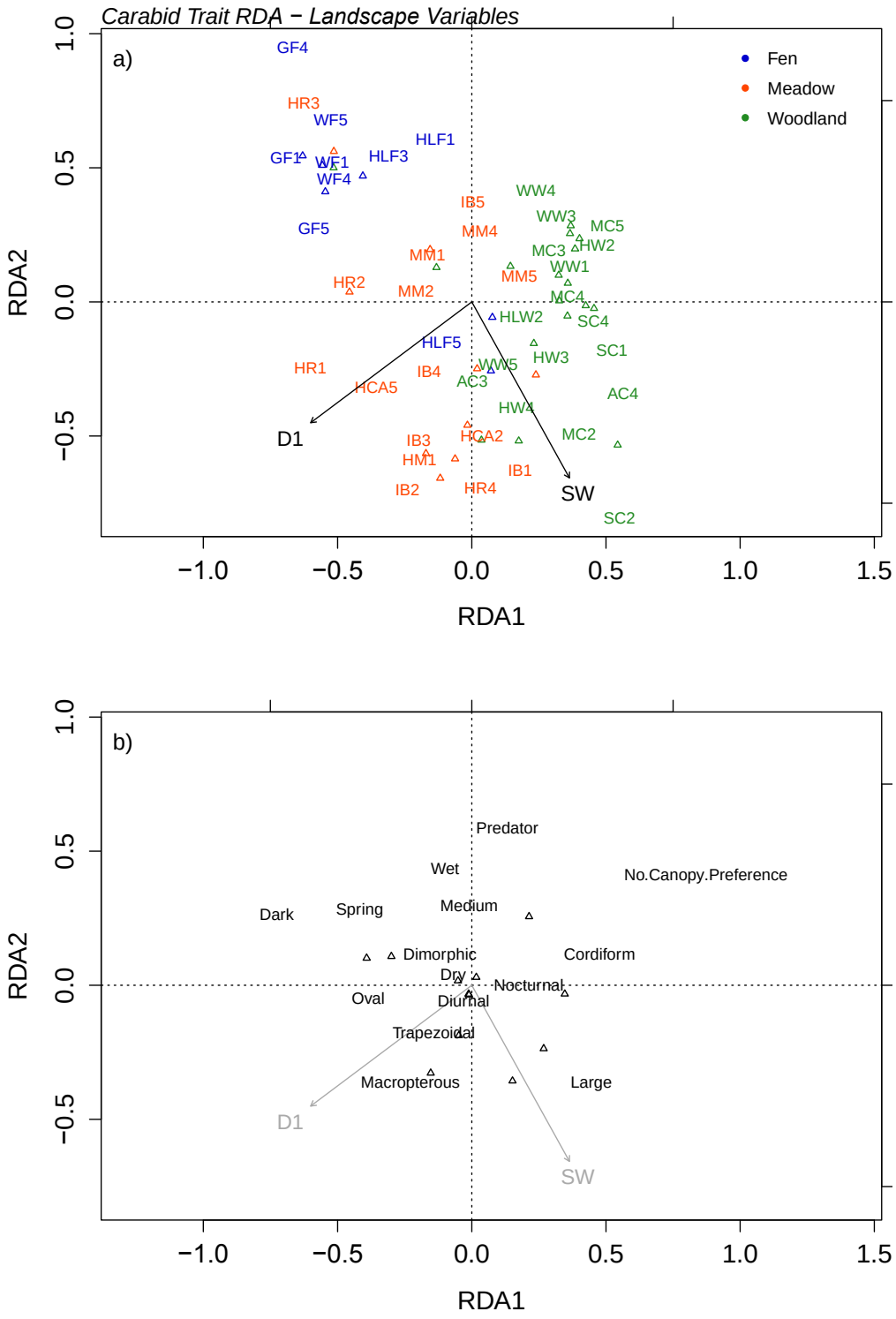


Figure 6.10 Redundancy analysis (RDA) of carabid assemblages at the macrohabitat scale according to functional traits and in relation to landscape variables. Plots in a) are labelled according to their site name and colours represent the different habitat types. Arrows represent significant landscape variables: D_1 (surrounding landscape complexity) and SW (surrounding woodland). Traits are labelled in b). Labelling priority is given to those traits that are most abundant using the inverse of Simpson's diversity index. Those traits not labelled are marked as an open triangle.

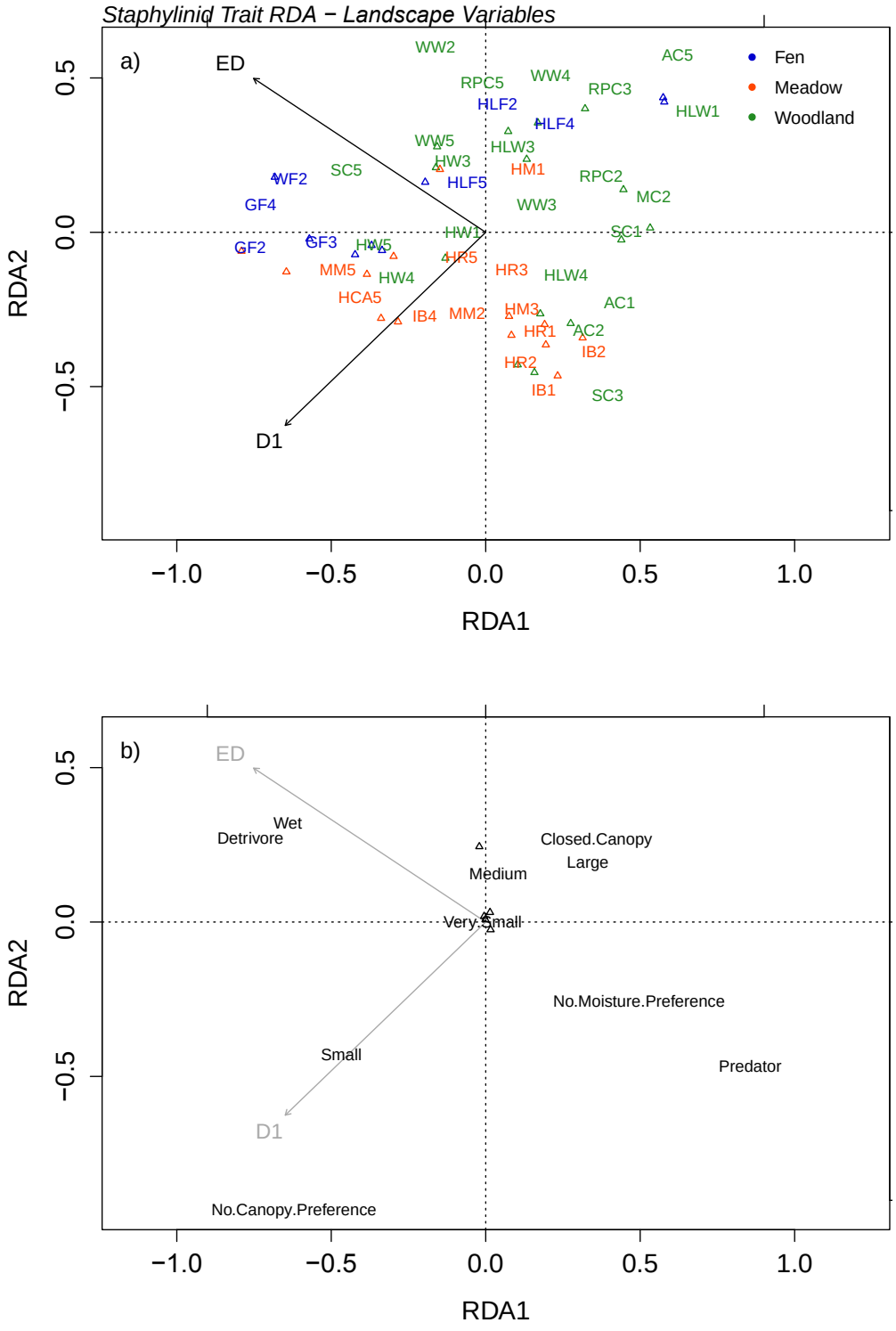


Figure 6.11 Redundancy analysis (RDA) of staphylinid assemblages at the macrohabitat scale according to their functional traits and in relation to landscape variables. Plots in a) are labelled according to their site name and colours represent the different habitat types. Arrows represent significant landscape variables: ED (edge density) and D_1 (surrounding landscape complexity). Traits are labelled in b). Labelling priority is given to those traits that are most abundant using the inverse of Simpson's diversity index. Those traits not labelled are marked as an open triangle.

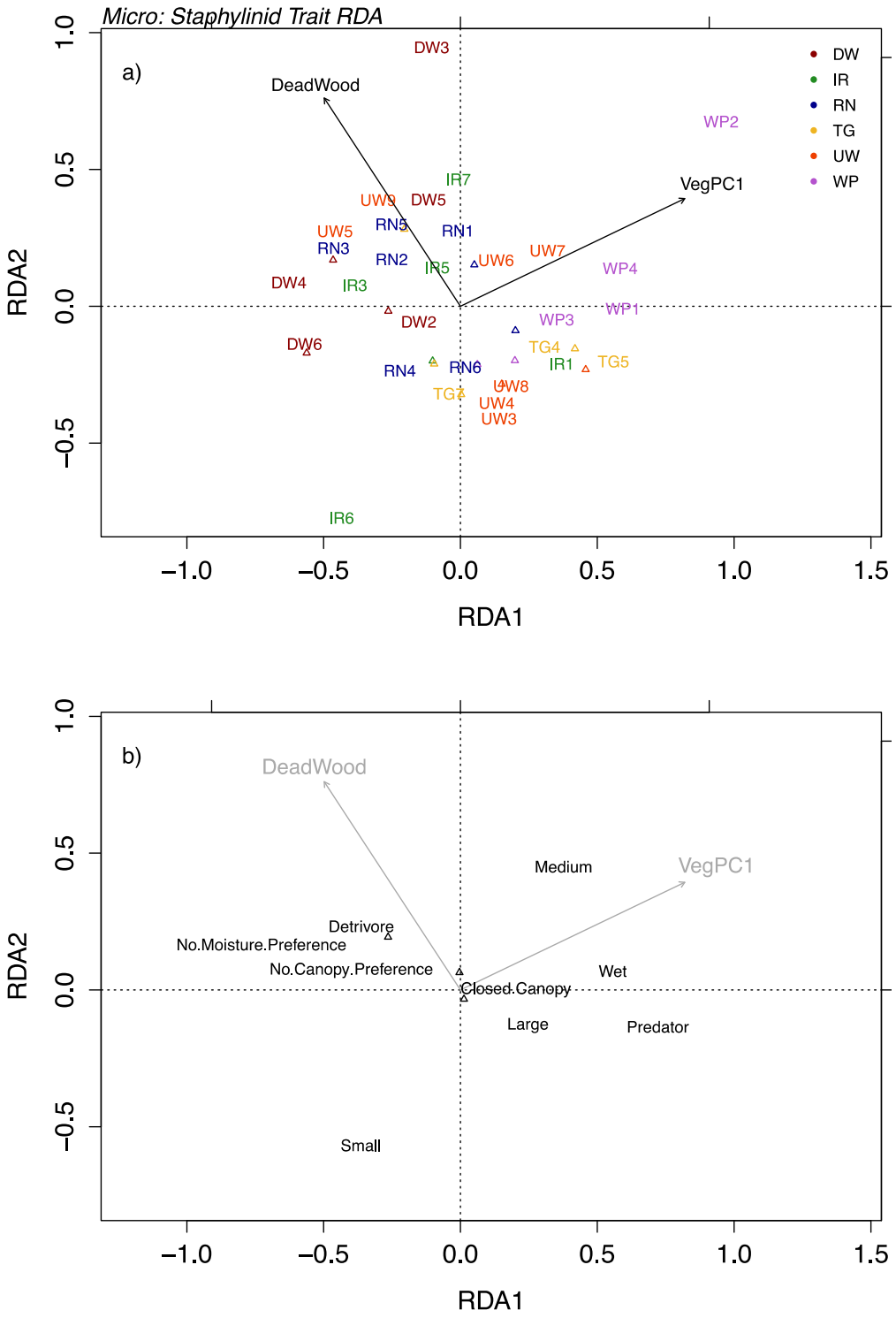


Figure 6.12 Redundancy analysis (RDA) of staphylinid assemblages at the microhabitat scale according to functional traits and in relation to microhabitat variables. Plots in a) are labelled according to their plot name and colours represent the different microhabitat types. Arrows represent significant microhabitat variables: Dead Wood and VegPC1 (vegetation species composition). Traits are labelled in b). Labelling priority is given to those traits that are most abundant using the inverse of Simpson's diversity index. Those traits not labelled are marked as an open triangle.

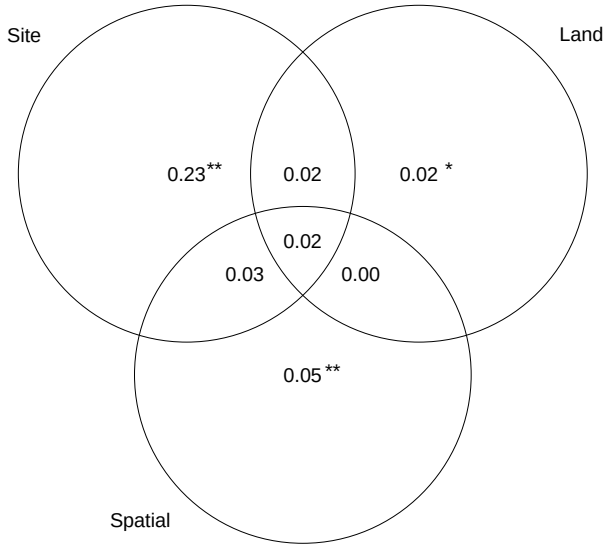


*Figure 6.13 Variance partitioning of the relative influence of site factors, landscape factors and spatial location on carabid trait assemblage composition. Values represent adjusted R^2 values, which are the proportion of variance explained by each component (total=1). The significance of each calculation after 9999 permutations is shown as ** <0.01, * <0.05.*

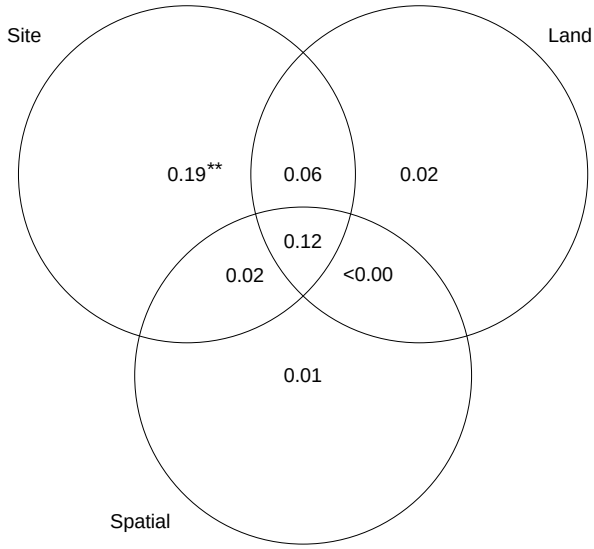


*Figure 6.14 Variance partitioning of the relative influence of site factors, landscape factors and spatial location on staphylinid trait assemblage composition. Values represent adjusted R^2 values, which are the proportion of variance explained by each component (total=1). The significance of each calculation after 9999 permutations is shown as ** <0.01, * <0.05.*

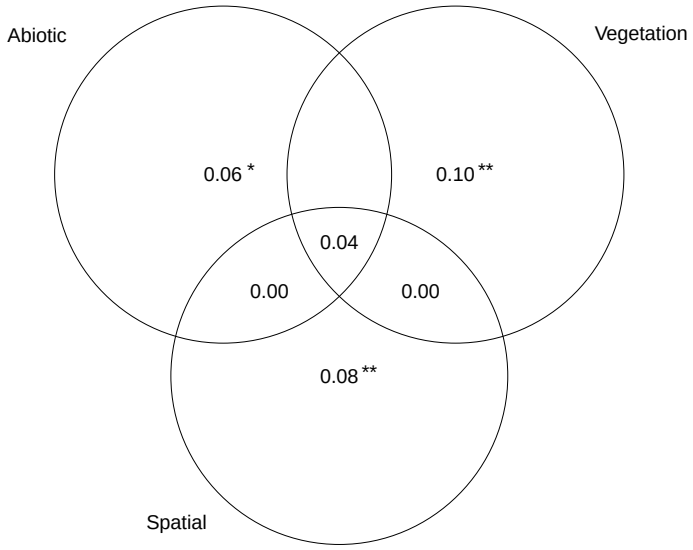


*Figure 6.15 Variance partitioning of the relative influence of abiotic factors, vegetation composition and spatial location on staphylinid trait assemblage composition at a microhabitat scale. Values represent adjusted R^2 values, which are the proportion of variance explained by each component (total=1). The significance of each calculation after 9999 permutations is shown as ** <0.01, * <0.05.*

Relationship between assemblages: taxonomy versus traits and carabid versus staphylinid beetles

A single significant relationship was identified between the three species-diversity indices and the four functional diversity indices in Pearson correlation tests: staphylinid F_{Ric} was positively correlated with Fisher's-α measurements (R=0.56, p=0.03). Procrustes analysis correlations between macrohabitat assemblages defined by taxonomy and those defined by functional traits were significant (Table 6.5). These relationships were also largely independent of environmental constraints, suggesting that sampling plots with unique species assemblages also support specific functional trait combinations. The relationships can be visualised by the relatively short distances between dots and arrowheads particularly for carabid ordinations in Figure 6.16. However, at microhabitat scales (Figure 6.16 e and f), the correlations between species and trait data were not as strong, and the inclusion of constraining environmental variables weakened the relationship further, suggesting that the distribution of species traits within the Alder Carr site, where these investigations were based, were not similar to the distribution of species. Procrustes diagrams indicate that this dissimilarity is nonetheless strongly driven by only a few, highly dissimilar plots. Finally, comparison of carabid and staphylinid trait assemblages showed a correlation of 0.44 ($p<0.01$; Table 6.5), while the ordination plot shows some distance between the carabid and staphylinid ordinations (Figure 6.17).

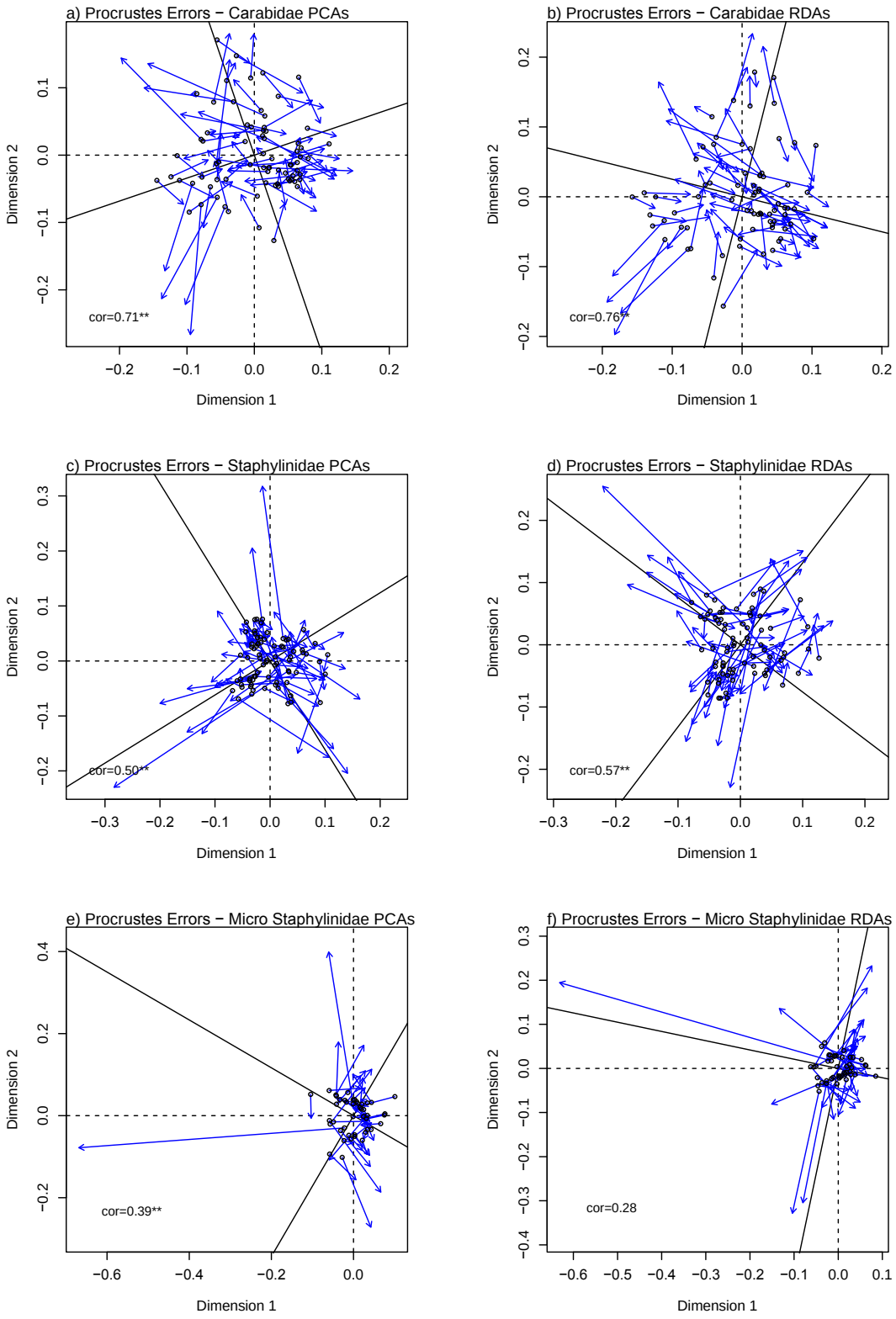


*Figure 6.16 Procrustes analysis ordinations of macro- and microhabitat plots comparing assemblages according to taxonomy and according to functional traits. Procrustes rotations were performed on models both unconstrained (PCA) and constrained (RDA) by environmental parameters, to assess the influence of environmental parameters on the relationships. 'Cor' is the correlation coefficient, the significance which, after 9999 permutations, is shown as ** <0.01, * <0.05.*

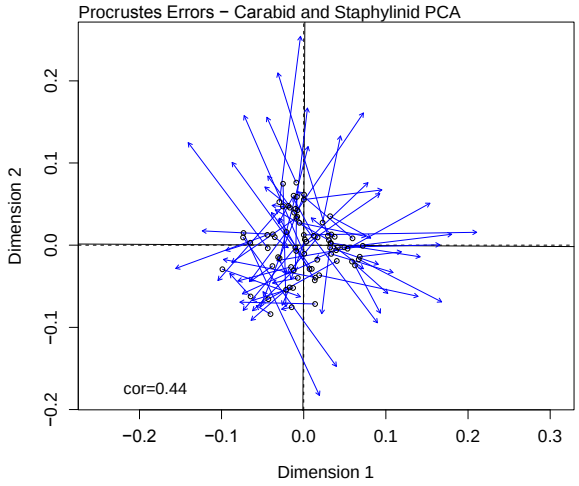


*Figure 6.17 Procrustes analysis ordination of plots comparing carabid and staphylinid functional trait assemblages. Dots describe the ordination of the plots according to carabid trait composition, whereas arrowheads show the ordination according to staphylinid trait composition. 'Cor' is the correlation coefficient, the significance which, after 9999 permutations, is shown as ** <0.01, * <0.05.*

Table 6.5 Procrustes rotation analysis results between species and trait matrices. 'Correlation' represents the correlation coefficient between the Procrustes rotations and 'p' is the significance of each calculation after 9999 permutations. Significant results are also marked in bold.

Procrustes analysis	Correlation	p	Procrustes SS	Root mean squared error
Macrohabitat scale				
Carabid species and trait PCA	**0.71**	<0.01	0.50	0.08
Carabid species and trait RDA	**0.76**	<0.01	0.42	0.07
Staphylinid species and trait PCA	**0.50**	<0.01	0.75	0.10
Staphylinid species and trait RDA	**0.57**	<0.01	0.68	0.09
Carabid and staphylinid trait PCA	**0.44**	<0.01	0.81	0.10
Microhabitat scale				
Staphylinid species and trait PDA	**0.39**	0.01	0.85	0.14
Staphylinid species and trait RDA	0.28	0.06	0.92	0.14

6.4 Discussion

6.4.1 Functional traits of floodplain beetle communities

As dynamic ecotones linking aquatic and terrestrial ecosystems, floodplain environments can host diverse fauna with specialised and adapted traits (Andersen & Hanssen, 2005), and are associated with many rare and stenotopic species (Lott, 2003; Sadler *et al.*, 2004; Lambeets *et al.*, 2008). In accordance with this, functional divergence measurements for all macrohabitat types was approaching a maximum, suggesting that these habitats all host highly diverse sets of functional traits. However, despite functionally diverse communities, the dominance of generalist species in relation to moisture and canopy density preference was notable. These versatile species, many of which have dispersal capabilities, may be favoured by their capacity to rapidly exploit a range of available resources and as such be favoured by the complex landscape encompassing these floodplain environments (Bettacchioli *et al.*, 2012).

One would predict that the environmental conditions of each floodplain habitat would match the functional traits of the organisms within, in accordance with the habitat templet theory (Southwood, 1977, 1988; Townsend & Hildrew, 1994). Accordingly, anthropogenic management activities could be expected to further alter the functional characteristics of a community because it disturbs and alters the habitat that acts as a templet for certain species traits (Resh *et al.*, 1994; Figure 6.18.a). While this may explain a number of the patterns identified in this study, many species with categorised traits showed no preference to the different floodplain habitat types. It has been stipulated that a match between a species' traits and the habitat in which that species lives may not occur on two grounds (Townsend & Hildrew, 1994): firstly due to the history of the environment combined with dispersal abilities of a species masking the effect of a habitat templet, or secondly due to species interactions of competition and predation, that may interfere with the relationship between templet and functional traits (Resh *et al.*, 1994; central gradient in Figure 6.18.a). As highlighted in previous chapters, the historical and contemporary management of many study sites has been inconsistent, which may have affected the match between functional traits of communities and habitat type. In addition, species' functional traits may be suitable or adapted to perform in several different habitats. The dominance of species with no preference to moisture or canopy conditions supports the suggestion that many species are adapted to a range of floodplain habitats across the habitat spectrum studied here and therefore may show no clear affinity to specific habitats.

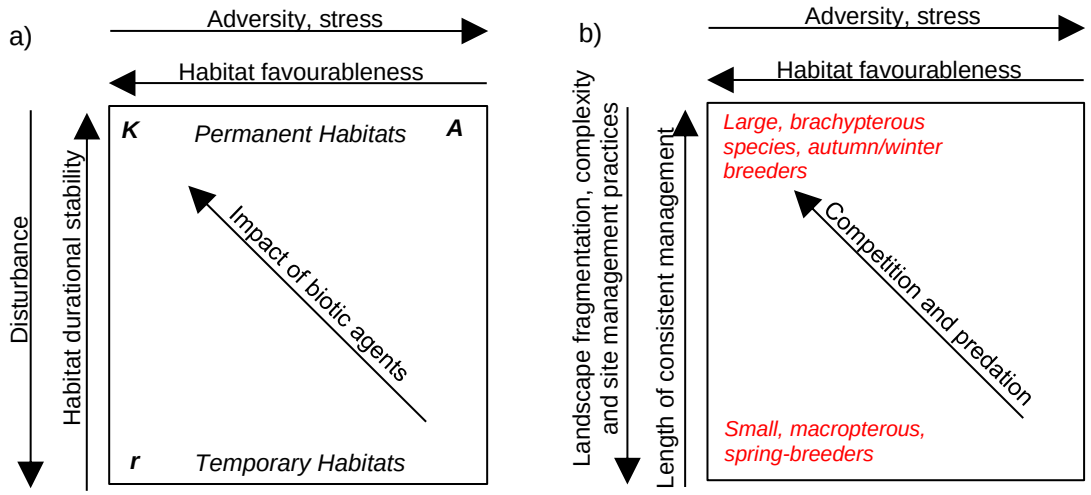


Figure 6.18 The habitat templet theory: a) according to (Southwood, 1988) and b) as applied to the results of this study. In a) 'K' represents organisms that invest a larger proportion of their resources into long-term survivorship and are therefore favoured in more stable habitats, and 'r' represents organisms that invest their resources into reproduction and dispersal, and are therefore related to more disturbed habitats. 'A' organisms are those adapted to very stressful environments such as montane habitats and were therefore not applicable in the context of the study results.

Although in many cases, the direct relationships between functional traits and habitat type were weak, a number of quantitatively important traits were apparent in floodplain beetle assemblages. These can be explained in part by the habitat templet theory; notably the traits size, dispersal, breeding season and trophic guild. The introduction and intensification of anthropogenic influences in ecosystems has been shown to be particularly damaging for large beetles (Blake *et al.*, 1994; Ribera *et al.*, 2001; Blake *et al.*, 2003; De La Peña *et al.*, 2003; Bettacchioli *et al.*, 2012). Large species have been associated with more stable systems because of their long life cycles and often weak dispersal ability (Blake *et al.*, 1994; Kotze & O'Hara, 2003; Rainio & Niemelä, 2003; Irmler *et al.*, 2010). This was mirrored by the findings of this study, as both large carabid and staphylinid species were primarily associated with woodland habitats experiencing low anthropogenic disturbance regimes. Comparatively smaller species, which characteristically exhibited short life cycles, fast development and often strong dispersal abilities, were associated with meadow and fen habitats that were subject to disturbance by cutting and grazing regimes. This trend also relates to the habitat templet theory which suggests that more disturbed sites favour *r*-selected organisms that invest their resources into reproduction and dispersal, whereas more stable environments such as woodlands favour *K*-selected organisms that invest a larger proportion of their resources into long-term survivorship rather than for example into good flight ability (Southwood, 1988; Lott, 2003; Figure 6.18.a).

Correspondingly, this also explains the support of higher proportions of brachypterous and apterous species in more stable woodland habitats than in more heavily disturbed floodplain meadows and fens. Den Boer (1977), Assmann (1999), Driscoll and Weir (2005) and Irmler *et al.* (2010) have all shown that old stable closed-canopy habitats are inhabited by many carabid species with low dispersal abilities. In comparison species in highly disturbed environments, such as those subject to cutting and grazing regimes, may have an elevated risk of local extinction and therefore also have an elevated need for good dispersal capabilities (Southwood, 1977, 1988; Ribera *et al.*, 2001). Brachypterous species are also often less well represented in fragmented landscapes, as they can only colonize new areas of suitable habitat by walking (Ribera *et al.*, 2001; Gobbi & Fontaneto, 2008). In this study, woodlands were fragmented within catchments, yet brachypterous or apterous species made up on average a third of the woodland assemblages. Given the aforementioned trends, it is possible that historically, this figure was considerably higher.

Breeding season and subsequent overwintering strategies are important factors that affect the survival of carabid populations due to varying vulnerability at different stages of their life cycle (Rainio & Niemelä, 2003). Carabid larvae are more susceptible to damage than adults (Blake *et al.*, 2003), and therefore, overwintering larvae may be more vulnerable to spring management regimes (Ribera *et al.*, 2001; Lott, 2003). Accordingly, breeding season followed a similar pattern to size and dispersal with this study, showing a clear habitat-related differentiation, where spring breeders were more prevalent in disturbed fen and meadow habitats subject to spring cutting and grazing, and autumn and winter breeders in less disturbed woodland habitats.

Finally, a distinct association of detritivorous staphylinids to fen habitats was evident, whereas predatory species were more commonly associated with meadow and woodland habitats. While there is little literature outlining the relationship between staphylinid feeding guilds and different wetland habitats, the high level of decaying plant material in the fen habitats was apparent (Figure 6.19). The tall vegetation characteristic of these floodplain environments is often cut or grazed (McBride *et al.*, 2011), but these management techniques can still leave substantial levels of decaying vegetation whether the site is grazed (Figure 6.19.a), left without management for a period of time (Figure 6.19.b) or subject to cut-and-rake regimes where not all cut vegetation is removed (Figure 6.19.c). This provides an abundance of dead and decaying biomass, which therefore relates to an abundance of food for detritivorous species.

Figure 6.19 The abundance of decaying plant material on fen sites providing food resource for detritivorous species. a) Wildflower Fen after grazing by donkeys in 2009, b) Wildflower Fen with no management for a year in 2010, and c) Glaven Farm after a cut-and-rake regime.

There was an evident common response of certain carabid trait groups to the same environmental gradients, particularly disturbance, which may allow for the definition of functional groups (Cole *et al.*, 2002; Driscoll & Weir, 2005; Bettacchioli *et al.*, 2012). Links between morphological and ecological characteristics of species are inevitable as species develop adaptations to their environment. For example, feeding behaviour has been extensively linked to the morphology of eyes, which can relate to particular predation techniques (Bauer, 1981; Bauer & Kredler, 1993). Similarly, links between the elytra colouration and a beetle's desiccation tolerance have been suggested, with more metallic species associated with drier habitats (Desender, 1989). Trait combinations or 'tactics' (Southwood, 1988) effectively adapt species to environmental stresses crucial for their survival in the templets within which they persist (Lambeets *et al.*, 2008). In the case of my study, landscape fragmentation, complexity and management practices therefore provide a disturbance gradient along which large, brachypterous autumnal breeders persist in more stable habitats and small, macropterous and spring-breeding species persist at the habitats experiencing high

disturbance levels through grazing or vegetation cutting (Figure 6.18.b). These trait combinations are very relevant in light of conservation biology, as they firstly provide a more mechanistic explanation of ecosystem processes and stability to inform conservation practices (Bengtsson, 1998), and secondly highlight the susceptibility of species and communities to anthropogenic disturbance (McKinney & Lockwood, 1999; Ribera *et al.*, 2001; Barbaro & Van Halder, 2009).

While the proportion of species traits represented at each site and habitat allowed the quantification of trait responses, functional diversity indices give a signal of underlying functional community structure. Lower levels of functional evenness and functional divergence were found within woodland habitats, a trend that indicates a low level of niche differentiation and high resource competition (Mason *et al.*, 2005). This pattern corroborates with the habitat templet theory, which implies that the highest level of biotic interactions and inter- and intra-specific competition occurs within habitats experiencing low levels of disturbance (Southwood, 1988; Townsend & Hildrew, 1994; Figure 6.18).

6.4.2 Influence of anthropogenic and environmental factors on community functional traits

Area, grazing and cutting, landscape complexity and edge density were the most important site and landscape variables driving the variation of carabid and staphylinid functional traits. These variables can be considered as the filters that constrain the combination of species' 'response traits' and enable the persistence of a particular functional community (Keddy, 1992; Violle *et al.*, 2007).

Within fragmented landscapes such as many UK and European floodplains, a number of traits have been linked with habitat patch area, including dispersal and size. Interconnected with the species-area relationship of island biogeography in which extinction rates are often negatively related to area (MacArthur & Wilson, 1967), one can expect that the smaller an area, the higher the proportion of species with good dispersal abilities (De Vries *et al.*, 1996) . Good dispersers, which are often small in size, are able to maintain populations in small isolated patches through re-colonisation of empty patches (Niemela, 2001), while on the other end of the spectrum, large habitats are stable enough and bear enough resources to support populations of very slow, weak dispersers (Bauer, 1989). Accordingly, larger areas within this study were

significantly associated with large, brachypterous carabid species, consistent with previous studies (De Vries *et al.*, 1996; Rainio & Niemelä, 2003).

Grazing and cutting regimes can be closely linked to the disturbance axis of the habitat templet concept (Figure 6.18.a). When the magnitude of disturbance is higher than a species or community can tolerate, only highly dispersive species will be able to persist in the habitat through repeated colonisation events (Ribera *et al.*, 2001; Lambeets *et al.*, 2008). This underlines the aforementioned significant influences of grazing regimes on staphylinid and carabid functional trait composition, and of cutting on carabid trait composition (Figure 6.18.b).

Finally, the significant links between species richness of both carabid and staphylinid communities on one hand and the vegetation composition on the other have already been identified within the context of this thesis for both beetle families, and within the wider literature (e.g. McCracken, 1994; Siemann, 1998; Siemann *et al.*, 1998; Blake *et al.*, 2003; Brose, 2003a). Such links may actually be associated with edaphic or management factors to which both plant and beetle communities are responding (Blake *et al.*, 2003). However, it must be noted that detritivorous species may be directly related to the amount of litter that becomes a source of food as it decays, whereas predators are more likely related to the herbivorous invertebrates on which the beetles prey and which might themselves be reliant on the vegetation composition and diversity (Siemann *et al.*, 1998; Woodcock & Pywell, 2009).

In addition to direct management practices, species assemblages in environments strongly affected by fragmentation are structured by their ability to act upon landscape disturbance (Lambeets *et al.*, 2008; Bettacchioli *et al.*, 2012). Landscape pattern has previously been identified as an important factor in driving the configuration of beetle assemblage traits (Jonsen & Fahrig, 1997; De La Peña *et al.*, 2003; Schweiger *et al.*, 2005; Batáry *et al.*, 2007). Since generalists may supplement their resource requirements by utilising more than one habitat type (Dunning *et al.*, 1992), they may benefit from a high diversity in surrounding land use types, which in turn results in an increased representation of generalists in habitats with complex surrounding landscapes (Jonsen & Fahrig, 1997; Batáry *et al.*, 2007). While this was illustrated with the negative association of closed canopy specialists with landscape complexity within this study, a further positive relationship with macropterous species highlights the importance of dispersal ability across these complex landscapes. Having the ability to disperse enables generalist species not only to exploit resources beyond a single site,

but also aids their effective dispersal to isolated habitat patches, as they are not affected by dispersal barriers due to shifts in habitat types. In turn, this strongly increases the effective ranges these species will occupy. For species with limited dispersal abilities, higher proportions of similar surrounding landscape may enable movement across fragmented landscapes, suggested within this study by the link between large carabids and percentage of surrounding woodland. Available woodland stepping stone habitats may enable the persistence of these large carabids in such complex landscapes. Finally, the influence of habitat fragmentation has been shown to affect different feeding guilds within beetle communities at different magnitudes, as demonstrated within this study. Carabid predators have been shown to respond more strongly to habitat fragmentation than phytophagous species, which actually appear to benefit from surrounding landscape diversity and particularly by the presence and extent of semi-natural grasslands (Davies *et al.*, 2000; Ribera *et al.*, 2001; Weibull *et al.*, 2003; Gobbi & Fontaneto, 2008; Barbaro & Van Halder, 2009). Within this study, habitats with low edge densities (small perimeter to area ratios) supported large proportions of predators, exemplifying the negative impact of habitat fragmentation on this feeding guild.

While landscape factors exerted a significant influence on beetle functional traits, variance partitioning clearly highlighted the dominant influence of site factors in the studied habitats, which suggests that site management is a fundamental controller of the functional traits of beetle assemblages in floodplain habitats. This contrasts to previous research in agricultural landscapes that highlighted a dominance of landscape factors on the trait composition of beetles and other arthropod communities (De La Peña *et al.*, 2003; Aviron *et al.*, 2005; Schweiger *et al.*, 2005). Future consideration of the dispersal abilities, breeding season and body shape of staphylinids may reveal a clearer picture of the contribution of macrohabitat scale processes on beetle functional traits in floodplain environments.

6.4.3 Variations in functional traits at a microhabitat scale

At a microhabitat scale, a very different picture emerged in relation to the trait composition in the staphylinid beetle assemblages, where differences in traits and trait diversity between microhabitat types were notably limited. While this could suggest that, at this spatial scale, species were not confined to specific habitats and that beetles may be too active for one to distinguish between functional groups, other studies have indicated otherwise. Lassau *et al.* (2005) found discrete responses of certain beetle

feeding guilds to different microhabitat components, with detritivorous species preferring habitats with more leaf litter, and fungivorous species being more abundantly trapped in sites with greater ground herb cover, most likely reflecting their foraging habits. However, they also noted that predatory subfamilies of staphylinids showed no significant microhabitat preference, potentially because, as generally active predators, this feeding guild is less specialized and can therefore utilise a greater range of habitats whilst foraging (Lott, 2003). Within this study, there was an association between detritivorous species and high concentrations of dead wood, but similar to Lassau *et al.* (2005) there was no clear association between other microhabitat elements and the remaining feeding guilds, including predatory species.

As relationships between habitat and species traits are dependent on the traits analysed, a likely explanation for a lack of significant responses at the microhabitat scale could also be the limited selection of staphylinid species traits used to analyse functional diversity. Dispersal ability, breeding season, diel activity, seasonal activity and other ecological and morphological characteristics may provide more substantial differences between microhabitat, but this information proved very difficult to obtain for individual staphylinid species. Within floodplain habitats, an increased frequency with proximity to water's edge has been demonstrated for macropterous carabids (Desender, 1989; Bonn & Kleinwächter, 1999), where these species can exploit temporary habitats caused by flood disturbance. Additionally, distributions in body size spectra have been demonstrated to change at the microhabitat scale (Barton *et al.*, 2011a), with larger carabid species found to be associated with closed canopy microhabitats. Continuous trapping over an entire field season to collect more substantial sample sizes of carabid and staphylinid specimens for analysis, combined with a focussed study of each specimen's wing development, may provide more specific explanations for functional trait assemblages at this microhabitat scale. Such research may also provide a stronger basis for understanding the dominant influence of vegetation composition on functional trait distribution.

6.4.4 Conservation implications

Species diversity versus functional diversity

Measurement of species diversity and the taxonomic associations of species with ecosystems dominates community ecology studies (McGill *et al.*, 2006) and subsequently conservation targets but, as demonstrated within this study and in the wider literature, species diversity is not necessarily linked with functional diversity or

species' functional traits (Diaz & Cabido, 2001; Ewers & Didham, 2006; Clough *et al.*, 2007; Bettacchioli *et al.*, 2012). While species diversity studies can identify declines in species and compositional analysis can identify factors causing those declines, functional diversity studies integrate biological differences among species and therefore can add an additional dimension to explain why certain species are more prone to decline than others (Henle *et al.*, 2004). For example, Kotze and O'Hara (2003) identified body size and dispersal abilities to be linked to the general decline in carabid species across Europe over the last 50-100 years. Knowledge of functional traits particularly sensitive to habitat loss and fragmentation, such as size and dispersal ability, can also prove especially useful when identifying target beetle groups for conservation practices (Davies *et al.*, 2000; Ewers & Didham, 2006; Barbaro & Van Halder, 2009).

The conservation of species is not just implemented to reduce species loss, but also to protect the services and functions species and communities provide (Cadotte, 2011). Yet, the majority of conservation policies focus on patterns of species richness, without considering how similar or different these species are in their ecological traits (McGill *et al.*, 2006). The use and comparison of species richness across different habitats or along environmental gradients implicitly assumes that all species are equal with respect to functioning in an ecosystem and all hold equal importance (Bengtsson, 1998; Mouchet *et al.*, 2010). However, an increased number of species could, for example, be generated by a strong increase in an assemblage of generalist predators masking a substantial loss of other feeding guilds, such as detritivores, within a habitat. Wide ranging declines in abundances of certain beetle species have been highlighted (e.g. Brooks *et al.*, 2012), but a loss in species performing certain functions or a substantial imbalance in the functional guilds, may result in a number of detrimental consequences, including changes in food webs, shifts in functional groups and their dynamics, loss of specialist functions, loss of keystone species and loss of ecosystem engineers (Moore *et al.*, 1988; Bengtsson *et al.*, 2000; Snyder & Evans, 2006).

An additional consideration for the use of functional diversity in conservation is the comparability among different spatial locations. Adopting a functional approach rather than focussing on taxonomic distinctions allows for comparisons of assemblages among different geographical locations as this is not reliant on common indicator species (Cole *et al.*, 2002). As such, adopting a functional trait approach for comparative ecological studies of floodplain habitats across Europe and across gradients from widely pristine to intensively managed habitats, could further

determine the influence of anthropogenic disturbance on these habitats and their ecosystem functioning, effectively enabling insights into benchmarks for restoration practices.

While the importance of functional diversity in conservation is apparent, consideration needs to be directed towards its measurement (Bengtsson, 1998; Naeem & Wright, 2003; Mason *et al.*, 2005; Petchey & Gaston, 2006, 2007; Violle *et al.*, 2007; Villéger *et al.*, 2008). In particular, deliberation is required for the selection of appropriate functional traits, indices and multivariate methods to tackle individual research questions and survey particular habitats studied (Gitay & Noble, 1997; Kleyer *et al.*, 2012). The use of inappropriate traits or a large number of traits can cause problems in the calculation of indices (Petchey & Gaston, 2007; Villéger *et al.*, 2008). If functional diversity measurements are to be used in conservation and restoration practices, well-planned, practiced and ecosystem-specific approaches need to be applied.

Restoration using functional diversity

In the monitoring and evaluation of ecosystem restoration, a functional approach may be particularly pertinent. Research has shown that restoring semi-natural habitats such as floodplain meadows using original management practices may not suitably restore the functional diversity of communities within these habitats when compared to pristine 'counterparts' (Woodcock *et al.*, 2011). The time scales to which species respond to restoration activities may differ according to their functional traits for a number of factors like colonisation ability, habitat stability and resource development. Within this study, different responses to habitat fragmentation variables have been noted, in particular for species of different sizes and dispersal abilities. The restoration of habitats may promote the colonisation of macropterous species that can easily disperse to take advantage of empty niches. However, large species with limited dispersal activity may be under-represented in restored habitats over prolonged periods of time, if not completely prevented from colonising these areas. Additionally, some functional groups have demonstrated clear association with stable woodland environments (Figure 6.18.b). Until suitably stable environments are established, these species can be expected to be missing from the trait spectrum. Linked to this is the time for resources to accumulate. Saproxylic and fungivorous beetles may be slow to colonise restored habitats due to the time needed for their food resources to establish (Gibb & Cunningham, 2010). While the functional diversity indices used in this study did not provide substantial signals between different habitat types, an assessment of functional richness, dispersion and evenness before and after restoration activities

may be a more suitable measure of the 'health' of an assemblage in comparison to, for example, species richness measurements.

Conservation of floodplain habitats

As highlighted throughout this thesis, the loss of floodplain woodlands and associated species is of upmost concern in Britain (Peterken & Hughes, 1995; Peterken & Hughes, 1998; Hughes *et al.*, 2001; Maddock, 2008) and other regions across the world (e.g. Rood & Mahoney, 1990; Hughes & Richards, 2003; Andersen & Hanssen, 2005). The low proportion of closed canopy specialists identified in the floodplain woodlands studied suggests that the UK lowland chalk river floodplains may have already lost many species naturally associated with these habitats. It also signals a rarity of true woodland specialists in the remnant floodplain woodlands (Hammond, 1998). Floodplain woodlands represent an ecosystem in need of urgent preservation, based on the sensitivity of species' functional groups they support. Habitat fragmentation has accelerated the selection of macropterous species against those with limited dispersal abilities, leaving species with low powers of dispersal and potentially an inability to compensate for population extinctions by (re)colonisation of other habitats (Den Boer, 1990b). Without measures to conserve large, wetland, brachypterous/apterous and autumnal breeding species characteristic to woodlands, these functional groups may be doomed in floodplain landscapes. However, restoration of these habitats may indeed be inadequate as connectivity of forests on floodplains is limited, and crossing non-forested area may not be possible, preventing successful colonisation by large species with restricted mobility in newly created habitat patches. Finally, studies have shown that low mobility species reach their highest richness in forests larger than 100ha and older than 130 years (Irmler *et al.*, 2010). Upon such knowledge, restoration seems a rather limited option for the conservation or floodplain woodland specialist species, but to adjust for these truths, long-term evaluation programmes should accompany restoration practices to measure the colonisation of woodland specific functional groups.

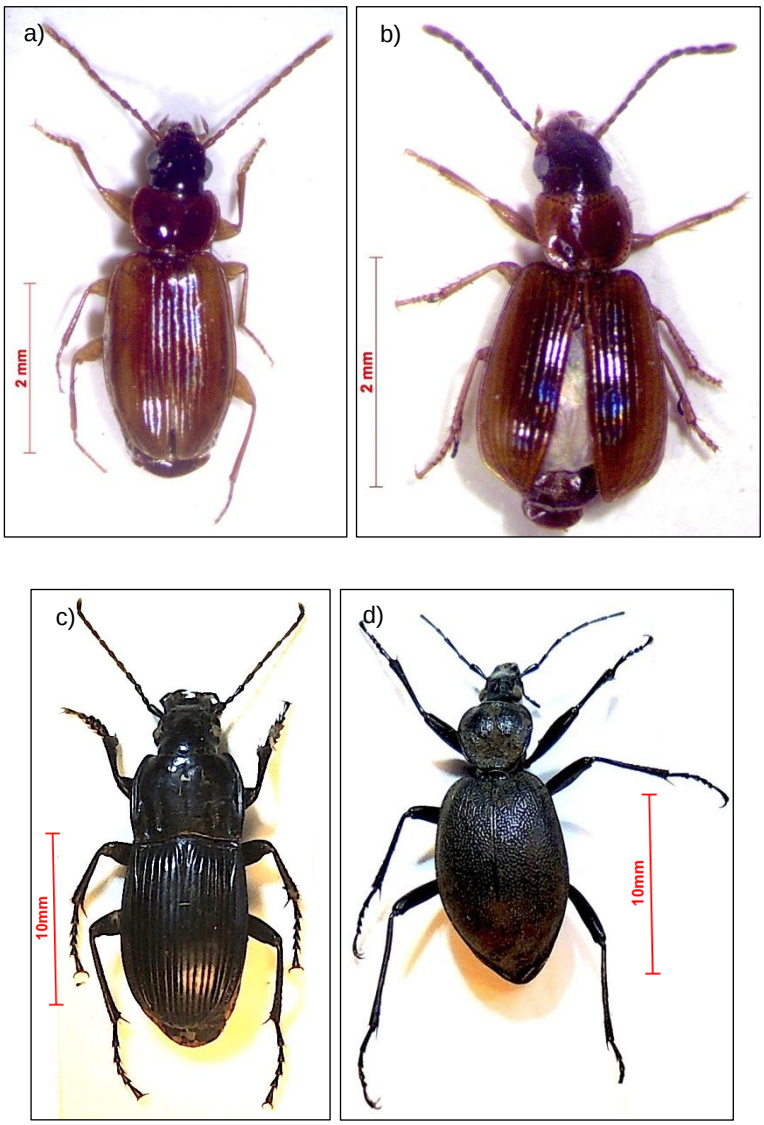


Figure 6.20 Examples of small macropterous species potentially favoured by habitat fragmentation and anthropogenically disturbed habitats, a) Trechus quadristriatus and b) Acupalpus parvulus, as opposed to large apterous species, which are associated with closed canopy, stable habitats with larger areas, c) Abax parallelepipedus and Cychrus caraboides.

While woodland habitats specifically may be an important floodplain conservation priority to safeguard full functional diversity of terrestrial beetles in river catchments, the association between habitat type, management practices and vegetation composition with a range of beetle functional traits suggests that a representation of different habitats within a floodplain landscape will increase the overall functional diversity of the landscape. By aiming for a heterogeneous landscape comprised of different habitat elements, whilst at the same time conserving large areas of specific habitat to ensure no functional trait extinctions, conservation in these landscapes can achieve a mix of functional diversity throughout the catchment. Furthermore, by

targeting habitat heterogeneity, it is more likely that biodiversity may be maintained throughout the food web together with other ecosystem services including nutrient recycling and pollination (Griffiths *et al.*, 2007)

Cross taxon functional diversity

A final consideration should be directed towards cross-taxon relationships within the context of this study. Based on a limited set of trait categories, carabid and staphylinid assemblages were significantly, but not very strongly correlated. Other studies have shown links between the functional traits of different taxa. For example Barton *et al.* (2011a) found trait associations and response to different environmental variables to be consistent across 35 different beetle families. Barbaro and Van Halder (2009) also found a consistent pattern in the distribution of life-history traits along the main gradients of disturbances for three different taxa: carabid beetles, butterflies and birds. Similar responses to environmental gradients across functional groups of different taxa could prove useful for conservation practices in recognising vulnerability of whole ecosystems. Additionally, links in functional traits between taxa are particularly important to consider in terms of food webs. For example, a number of bird species that feed on beetles will optimally seek to feed on larger species rather than a large number of small specimens (Blake *et al.*, 1994), in accordance with the 'size efficiency hypothesis' (Brooks & Dodson, 1965). As such, the disappearance of floodplain woodland habitats and with it a reduction in abundance of large beetles in the floodplain could have knock-on effects for floodplain bird communities (Wilson *et al.*, 1999; Cole *et al.*, 2002). The importance of different habitat types for different functional groups across different taxa should be considered for optimal conservation policies (Griffiths *et al.*, 2007). Yet, it should be noted that cross-taxon relationships may differ in other landscapes (Lambeets *et al.*, 2009), and therefore should not be relied upon without prior research into the overall distribution of trait spectra across taxa in these specific landscapes.

6.5 Conclusion

This study strongly contributes towards the understanding of the functional species traits of beetles in chalk river floodplain habitats and their response to environmental gradients and disturbance at differing spatial scales. It has demonstrated that characterising habitats beyond the number of species they can support can provide more comprehensive understanding to community and ecosystem ecology. Notably, due to the differences in species taxonomical composition and functional trait composition, when no signal of the influence of anthropogenic changes on alpha or beta diversity is identified, this may not mean no consequence has entailed. Functional responses can be accelerated and out of sync with species adjustments and should therefore be utilised in the ecological monitoring of ecosystems and in conservation and restoration practices. Finally, as one of the most biodiverse families of the ground macrofauna, more research into the traits of staphylinid beetles is urgently needed to help further understand responses of their communities to anthropogenic change in these sensitive floodplain environments.

Chapter 7. Summary, key themes, conclusions and future directions

The primary focus of this thesis was an investigation of the influence of anthropogenic and environmental changes on beetle communities in chalk floodplain habitats. Accordingly, chapters 3 – 6 presented analyses of carabid and staphylinid beetle assemblages in a range of chalk floodplain habitats in Norfolk, addressing different components of their diversity at different scales, and directly fulfilled each of the four research questions outlined on page 38. The major findings of this work are summarised below. This final chapter also considers the main themes of biodiversity conservation materialising throughout the thesis and concludes with future research directions.

7.1 Summary

The initial analyses presented in this thesis (**Chapters 3 - 4**) focussed on the relative influences of site and landscape-scale factors on beetle diversity and illustrated the degree of cross-taxa community similarities. **Chapter 3** in particular assessed the alpha diversity of 15 floodplain sites, comparing management types and the dominant site and landscape factors influencing beetle α-diversity. Using a combination of species estimators and α-diversity indices, the study revealed a lack of significant differences in the α-diversity of carabid and staphylinid beetles between habitats. Nonetheless, fen habitats showed consistently low α-diversity values. Considering the proposed high diversity of these habitats for a range of taxa (English Nature, 2005b; Middleton *et al.*, 2006; McBride *et al.*, 2011), and the high diversity of plant species recorded at these sites, this brought into question whether these small and fragmented floodplain fens can support high numbers of invertebrate species for which this habitat type is otherwise known and also highlighted the potential legacy of historic land use patterns on current communities. Within Chapter 3, multiple linear models revealed multiple differing site and landscape influences on the α-diversity of carabid and staphylinid

beetles and put into question the applicability of cross-taxon inferences in biodiversity research and conservation. Furthermore, inconsistent and weak relationships between beetle and vegetation α-diversity indices were revealed, highlighting the risks in current approaches to biodiversity conservation that commonly use vegetation-based surrogates to assess overall status of, and trends in, biodiversity. Finally, by investigating both species richness and α-diversity indices in the analysis of beetle communities, I highlighted the importance of the choice of good metrics in biodiversity studies and conservation practices, in terms of suitability for the taxon studied and the element of biodiversity in focus.

Leading on from the above, **Chapter 4** addressed the β-diversity of beetle assemblages in the same floodplain habitats, focussing on the relative importance of site management and the surrounding landscape patterns on beetle communities. In this study, multivariate analysis of variance revealed significant differences in beetle communities between habitat types. However, while habitats hosted different assemblages in terms of species composition, further analysis revealed that the overall heterogeneity across different habitats was similar, in that these floodplain habitats supported different but equally heterogeneous beetle assemblages. Overall, these findings are consistent with the wider literature, which emphasises the diverse nature of floodplain ecotones (Naiman *et al.*, 1993; Naiman & Décamps, 1997; Ward *et al.*, 1999; Tockner & Stanford, 2002). My analysis further revealed that anthropogenic influences at the site scale played the most significant role in structuring communities, namely the management type (habitat type, grazing and cutting), as well as the site area. This confirmed the importance of management decisions on beetle communities within these floodplain environments, and additionally the importance of sustaining suitably large areas to enable the persistence of habitat-specific communities. Furthermore, the influence of edge density, landscape composition and elements of the surrounding land use that I recorded, suggested that habitat fragmentation has influenced the beetle communities of these habitats and therefore should be considered alongside management in the conservation of floodplains. Despite responding to similar sets of anthropogenic factors, the relationships between carabid and staphylinid assemblages was not marked, raising further questions regarding cross-taxon links often assumed in biodiversity conservation. However, in contrast to α-diversity metrics, both carabid and staphylinid assemblage changes were correlated with shifts in vegetation composition, and although the causal mechanisms of these relationships cannot be disentangled and caution must be taken in the use of

vegetation as a surrogate for beetle diversity, it suggests that vegetation surveys may have the potential to indicate changes in the composition of beetle taxa. Finally, significant differences in beetle β-diversity spatially, and in particular between catchments for staphylinid beetles, highlighted the importance of connectivity within landscapes and confirmed that conservation practices need to be considered within the context of each catchment due to potential biogeographical differences.

In **Chapter 5**, I addressed the micro-scale beetle communities of a chalk floodplain forest in order to understand the distribution of communities at this scale and their response to microhabitat environmental gradients in remnant mature floodplain forests. α-diversity of carabid and staphylinid species showed no difference between microhabitat types, and β-diversity analysis on staphylinid beetles (the small number of carabid specimens collected preventing respective analysis) revealed no significant between-microhabitat differences, either. This contrasted to previous research, which suggested beetles can be associated with specific microhabitats according to their specialisations and adaptations (Niemelä *et al.*, 1996; Bonn & Kleinwächter, 1999; Koivula *et al.*, 1999; Antvogel & Bonn, 2001; Lott, 2003; Lassau *et al.*, 2005; Barton *et al.*, 2009). However, a number of reasons were suggested for the absence of such a relationship in this study, including a high abundance of generalist species, the fine mosaic of microhabitat types throughout the site and potentially a wider activity radius at which beetles utilise resources. Despite the absence of clear relationships, the high diversity of microhabitats found within this floodplain forest, in combination with the abundance and diversity particularly of staphylinid species sampled within the two-week sampling period, confirms that mature floodplain forests within Britain can still support a substantial diversity of beetle species. Furthermore, a recognised influence of vegetation composition and percentage cover of dead wood and twigs suggests that, while microhabitat elements may not be distinct, beetles do respond to microhabitat structure at these fine spatial scales. Therefore heterogeneity at microhabitat scales, including the presence of dead wood, should be promoted in the management and restoration of remnant floodplain forests.

A functional trait approach was utilised in **Chapter 6** to ascertain whether beetle community distribution and their responses to anthropogenic and environmental gradients could further be explained by the morphological, ecological and associated habitat traits of individual species. Literature on staphylinid functional traits was limited, emphasising the general need for further research in this area. At a macrohabitat scale, both habitat comparisons and multivariate analysis revealed the

association of certain beetle traits to different habitats, particularly in terms of more stable, shaded woodland systems compared to open, managed fen and meadow habitats. These findings echoed the main themes of the habitat templet theory (Southwood, 1988; Townsend & Hildrew, 1994) that suggests habitats act as a templet upon which the ecological sorting of species that occupy the respective habitat occurs. Floodplain fens hosted high proportions of wetland species, showing their potential to provide habitat to a unique set of wetland fauna. Analysis of the relative influence of different anthropogenic impacts revealed that site management practices and landscape fragmentation (patch area, patch edge density, landscape complexity and connectivity) provided a disturbance gradient along which large, brachypterous, autumnal breeders persist in more stable habitats and small, macropterous, spring-breeding species persist in habitats experiencing substantial human disturbances. This highlighted the vulnerability of certain species and functional trait groups to anthropogenic disturbance. While landscape factors were significant in influencing community trait compositions, variance partitioning clearly confirmed the dominant influence of site factors in these habitats, mirroring observations made in Chapter 4 for taxonomic groupings. In turn, this finding reinforced the notion that site management has a fundamental influence on beetle assemblages in floodplain habitats. At a microhabitat scale, differences in traits and trait diversity between microhabitat types were limited, which suggested that at this spatial scale, functional groups were not confined to specific microhabitats or that beetles may be too active to distinguish functional groups' habitat affinities at the very fine spatial scales considered here. It was concluded, however, that the limited selection of staphylinid species traits used to analyse functional diversity might have reduced the overall interpretability of the results. Carabid and staphylinid functional assemblages were significantly correlated, as has been found with cross taxa links in other functional diversity studies. Overall, the results cause concern regarding the effects of increasing habitat fragmentation on different animal and plant species groups that share vulnerable trait combinations. Links between functional and taxonomic diversity measurements were weak, highlighting the importance of adopting different biodiversity perspectives within conservation biology, which can together contribute to a more comprehensive picture of diversity within ecosystems.

7.2 Key Themes

7.2.1 Measuring biodiversity

A theme occurring throughout this research concerns the different approaches to measuring biodiversity. α- and β- diversity measurements for both characterisations of taxonomic and functional diversity have been addressed in previous chapters, and each of these approaches has provided an extra dimension to the understanding of floodplain beetle communities. The evident multidimensional nature of biodiversity means it cannot effectively be reduced into a single number (Purvis & Hector, 2000), yet maximizing species richness is often a clear or inherent goal of biodiversity conservation (May, 1988; Gotelli & Colwell, 2001). While α-diversity values can provide an intuitive index of community structure (Gotelli & Colwell, 2011), in the floodplain environments studied here, the limitations of species richness and other α-diversity measurements have been clearly revealed. Firstly, many α-metrics are highly sensitive to sampling effort (Axmacher *et al.*, 2008; Bonar *et al.*, 2011), with species richness estimators suggesting that only between 64% and 92% of species within the floodplain sites were included in the samples. It has been suggested that ecologists and conservation biologists have not always appreciated the influence of sampling effort on richness measures and comparisons (Gotelli & Colwell, 2001). This is a particularly important consideration with invertebrates where the sheer numbers of specimens within a habitat are impossible to collect completely, even with extensive sampling efforts. Where possible, efforts should be made to compare 'true' levels of species richness combining some of the methods shown in Chapter 3 in order to provide a realistic indication of biological diversity.

A second limitation of α-diversity measurements, as demonstrated within this research, is the reduction of a large amount of data into a single value. By their very nature, α-diversity measurements do not take into account differing species compositions within samples. Two samples with entirely different species, but with the same number of different species and the same abundance patterns would produce the same α-diversity value despite hosting very different communities (see Purvis & Hector, 2000). For example, no significant differences were recorded between habitat types across a number of different α-diversity measurements, whereas β-diversity analysis and indicator species calculations revealed strong differences in the underlying community compositions. This is a particularly significant limitation in

anthropogenically-altered environments, where habitat fragmentation can promote the prominence of generalists (Jonsen & Fahrig, 1997; Bettacchioli *et al.*, 2012), which may superficially maintain or inflate overall species richness levels whilst the loss of specialist species can be hidden.

A further comparison was made between taxonomic and functional approaches in biodiversity research and conservation. Whereas the assessment of taxonomic diversity provides information about species' declines and changes in community composition, functional diversity measurements go beyond this by relating differences in communities to the functional interactions of organisms with their environments (Cadotte, 2011). Functional diversity approaches thereby provide additional insights to understand the mechanisms underpinning the relationships between beetle assemblages, habitat change and landscape complexity (Lambeets *et al.*, 2009). Within this research, the adoption of a functional approach afforded an ability to explain questions such as why certain species are more prone to decline than others. It also helped to identify target groups for conservation practices and enabled comparisons of assemblages among different geographical locations. However, assessment of functional diversity for taxa within an ecosystem is very dependent on the functional categories used, the choice of which can considerably change the outcome of a study (Gitay & Noble, 1997; Petchey & Gaston, 2006).

Regarding the measurement of biodiversity in general, this thesis has revealed that reliance on one aspect of biodiversity, be it α- or β- diversity related to taxonomic or functional diversity, will not provide a complete representation of ecosystem biodiversity. Yet, a highly multi-dimensional approach to biodiversity investigations, which can be seen as the ideal approach, is not feasible in most cases. What is important in the measurement of diversity is the use of tailored and appropriate methods based on study objectives and conservation goals. For instance, if the aim is to conserve species vulnerable to anthropogenic change, functional diversity-based investigations allow the identification of specific trait combinations increasing a species' threat status and the respective set of vulnerable species, accordingly. Similarly, if cross catchment or regional comparisons are required, α-diversity metrics that do not take into account differences in the composition of species may be appropriate, and furthermore taxonomic approaches should again be underpinned by trait analyses, which enable comparisons to be made irrespective of biogeographical differences in taxonomic composition.

7.2.2 Scale

Two key concepts have been raised in relation to scale within this investigation: firstly the importance of measuring taxa at the scale relative to their habitat utilisation, and secondly to fully consider the scale at which taxa and entire species assemblages are affected by anthropogenic disturbances and environmental gradients. Biodiversity studies have often focussed on taxa at broad scales, as these are commonly the dimensions at which humans interact with their environment (Wiens & Milne, 1989; Hewitt *et al.*, 2010). Indeed, numerous studies have highlighted the bias towards vertebrates due to the scales at which they 'experience' habitats (e.g. Hafernik, 1992; Bonnet *et al.*, 2002; Magurran, 2004; Tews *et al.*, 2004). However, invertebrates such as beetles can utilise habitats at micro-scales. Furthermore, beetles commonly utilise up to five different microhabitats at their different life stages, namely as larvae, pupae, teneral adult, hibernating adult and active adult (Lott, 2003). Some species also show affinities to a whole range of different microhabitats throughout their adult life due to their respective breeding suitability, food availability and shelter (e.g. Niemela *et al.*, 1992; Bonn & Kleinwächter, 1999; Antvogel & Bonn, 2001; Brose, 2003b; Lassau *et al.*, 2005; Barton *et al.*, 2011a; Barton *et al.*, 2011b). While beetles within this study did not show affinity to the specific microhabitat types at the scales investigated here, it was recognised that consideration of the scale at which organisms utilise their habitat and interact should be considered, rather than restricting biodiversity studies and conservation practice to areas scaled to the human level of perception (Wiens & Milne, 1989).

As mentioned above, the second scale concept exposed in this research is nonetheless the scale at which beetles respond to anthropogenic and environmental gradients. Responses have been investigated at landscape, site and micro-scales within this study, with site scale influences exerting a dominant influence on beetle diversity. While invertebrate groups such as beetles may effectively indicate changes at the floodplain scales, at larger scales, such as 10km^2, responses of beetle species to anthropogenic disturbances is limited (e.g. Brose, 2003b). Many vertebrate species may serve as better indicators of wider landscape level changes, such as fragmentation that occurs at scales extending over several km^2 (Pearce & Venier, 2006).

7.2.3 Cross-taxon relationships

Conservation management approaches are moving beyond single species targets to focus on entire biological communities, considering multiple taxa at different scales

(Noss, 1990; Simberloff, 1998; Su *et al.*, 2004). These approaches often rely on the use of surrogate taxa whose diversity patterns are believed to be representative for entire sets of further taxa. Yet evidence suggests that correlations of species diversity patterns between pairs of taxa are highly variable (Prendergast *et al.*, 1993; Lawton *et al.*, 1998; Axmacher *et al.*, 2004a; Rodrigues & Brooks, 2007; Axmacher *et al.*, 2011; Gioria *et al.*, 2011) and may be dependent on scale (Weaver, 1995; Su *et al.*, 2004). Indeed, highly inconsistent cross-taxon relationships have been demonstrated between a range of different taxa and carabid and staphylinid beetles, respectively (Table 7.1), and these issues have already been highlighted in this thesis. Relationships identified between beetle families within this study also differed depending on the components of biodiversity in focus. At a taxonomic level, no congruence was uncovered between carabid and staphylinid beetle assemblages, yet functionally, the composition of these assemblages was positively correlated. Similarly, contrasting relationships were identified between beetles and vegetation dependent on the scale and element of biodiversity explored. Whether related to vegetation composition, structure or abiotic factors to which both plants and beetles respond, these varying responses confirmed that consistent conclusions cannot be drawn for relationships between beetles and vegetation. Additionally, in one example, the contrasting influence of past land use on plant and beetle taxa was evident, demonstrating that the historical land-use context and response times of individual beetle species and entire communities to land-use changes can further complicate underlying relationships between vegetation and beetle diversity.

In the realm of floodplain conservation where habitats are naturally highly heterogeneous (Ward *et al.*, 1999; Robinson *et al.*, 2002), variation in cross-taxon relationships again indicate that multiple approaches and measures of community structure are required for a comprehensive assessment of biodiversity (Gioria *et al.*, 2011). However, while carabid and staphylinid beetles may not suitably reflect one another in various measures of diversity, the protection of natural and long-established habitats such as mature floodplain woodlands based on their biodiversity alone is likely to be beneficial to other taxa. Furthermore, response to long-term anthropogenic changes in addition to immediate disturbances demonstrates the potential for beetle assemblages to inform biodiversity discourses beyond the limits of current land use practices.

Table 7.1 Examples of the variability of cross-taxa studies involving carabid and/or staphylinid beetles. '' represents an identified relationship between the two taxonomic or functional groups, whereas '' reflects no identified relationship.

	Taxonomic Approach		Functional Approach	
	Carabid beetles	**Staphylinid beetles**	**Carabid beetles**	**Staphylinid beetles**
Carabid beetles		Sætersdal *et al.* (2003)		Barton *et al.* (2011a)
Spiders	Sætersdal *et al.* (2003) Sauberer *et al.* (2004)	Sætersdal *et al.* (2003)		
	Bonn *et al.* (2002) Bonn and Kleinwächter (1999) Paetzold *et al.* (2008)	Paetzold *et al.* (2008)	Lambeets *et al.* (2009)	
Other invertebrates	Schuldt and Assmann (2010)	Sauberer *et al.* (2004)	Barbaro and Van Halder (2009) Barton *et al.* (2011a)	Barton *et al.* (2011a)
	Axmacher *et al.* (2011)			
Amphibians	Schuldt *et al.* (2009)			
	Oliver *et al.* (1998)	Oliver *et al.* (1998)		
Vertebrates	Schuldt and Assmann (2010)		Barbaro and Van Halder (2009)	
	Oliver *et al.* (1998)	Oliver *et al.* (1998)		
Plants	Barton *et al.* (2009) Blake *et al.* (2003) Koricheva *et al.* (2000) Schuldt *et al.* (2009) Schuldt and Assmann (2010) Sætersdal *et al.* (2003) Sauberer *et al.* (2004) Woodcock *et al.* (2005b)	Barton *et al.* (2009) Sætersdal *et al.* (2003) Woodcock *et al.* (2005b)	Cole *et al.* (2002) Koricheva *et al.* (2000)	
	Axmacher *et al.* (2011) Brose (2003a) Oliver *et al.* (1998)	Oliver *et al.* (1998)		

7.2.4 Conservation of chalk floodplain habitats in practice

Assessing conditions in the dominant habitat types along three Norfolk chalk rivers, this thesis has identified characteristic beetle assemblages in meadow, fen and woodland habitats and recognised important focal areas for conservation measures. Floodplain meadows have been subject to a lot of both conservation and restoration attention (Benstead *et al.*, 1997; Joyce & Wade, 1998; Blackstock *et al.*, 1999; Bissels *et al.*, 2004; Woodcock *et al.*, 2005b; Woodcock *et al.*, 2005a; Klimkowska *et al.*, 2007; Liira *et al.*, 2009; Woodcock *et al.*, 2011; Clilverd *et al.*, 2013). In particular, detailed research has been performed on the hydrology, ecology and nutrient cycles of these habitats (Gowing & Spoor, 1998; Gowing *et al.*, 2002; Barber *et al.*, 2004 and ongoing research by the Floodplain Meadows Partnership, www.floodplainmeadows.org.uk).

Extensive areas of fen land has been subject to conservation attention, for example Wicken Fen and Woodwalton Fen in Cambridgeshire and Baston Fen in Lincolnshire, which cover areas of 247 ha, 90 ha and 47 ha, respectively, and are all classified as SSSIs. However, small areas of remnant floodplain fens are often neglected in terms of studies and management (Hammond, 1998). These fen remnants may be difficult to manage in a traditional way, as it is not economical for farmers to graze small numbers of cattle for short periods of time. It has been suggested that this has contributed to the decline in floodplain fens within the Glaven catchment (local farmer, Ian Shepherd, pers. comm). Small remnant fen patches are of concern for conservation due to the potential presence of rare beetle species, inconsistent management and vulnerability due to their small areas. Left as such small remnants, they are furthermore strongly influenced by surrounding landscape composition and as such may no longer be able to harbour the high-diversity and fen-specific communities for which they are well known. While increasing the extent of these habitats may not always be possible in the current, agriculturally-dominated landscapes, maintaining some sort of connectivity between patches, ensuring continuous management and monitoring changes in communities is essential if fen-specific communities are to be conserved and enhanced in these fen fragments. Furthermore, consideration of managing these fragments at a wider landscape scale could help optimise resources (McBride *et al.*, 2011). Using a grazier for a number of sites in the same area on rotation may be more cost effective than cutting single sites throughout the landscape. Once ecological conditions are suitable within fen fragments, there is also the potential to re-introduce certain species of beetles and other insects into fen fragments, a technique that has been widely used

in the restoration of plant communities (Maunder, 1992; van Diggelen *et al.*, 2006; Klimkowska *et al.*, 2007), and has been considered for other invertebrates such as grasshoppers (Kiehl & Wagner, 2006).

The conservation importance and restoration potential of floodplain forests was another key focus of this thesis. These stable habitats were shown to host a highly heterogeneous mix of different microhabitats both in terms of vegetation and abiotic factors, and they additionally harbour species that share a combination of morphological and ecological traits making them highly vulnerable to anthropogenic disturbances. The spectrum of potential options for restoration has been highlighted in Chapter 5 and is shown in Table 7.2. Natural forest growth combined with connectivity to the river is an idealised option for floodplain forest restoration, yet still remains a possibility for lowland chalk rivers, where there is a current conservation focus. For example, the River Glaven is currently subject to considerable conservation management in particular, due to the great respective interest by local stakeholders organised within the River Glaven Conservation Group (RGCG). The RGCG was established in 1999 with the aims of protecting the river and its floodplains from pollution and degradation, whilst conserving and restoring important habitats for wildlife within the river corridor (River Glaven Conservation Group, 2013). The RGCG has been involved in a number of restoration projects in the past decade including the removal of embankments along two stretches of the river to re-establish river-floodplain connectivity. One of these sites was Hunworth Meadow, as included in this research (Figure 7.1). Since the bank removal works, natural flooding regimes have returned (Clilverd *et al.*, 2013), and in turn have enabled the deposition of seeds and propagules onto the floodplain at Hunworth Meadow from upstream woodland sources (Ward & Stanford, 1995; Nilsson *et al.*, 2010). This has led to the natural regeneration of vegetation including a prominent cover of alder (*Alnus glutinosa*) saplings adjacent to the river bank (Figure 7.2). Young alders can grow very rapidly during the first 5-10 years (Johansson, 1999), and combined with the potential for further provision of alder seeds and propagules from floodwaters and the presence of an adjacent woodland habitat, Hunworth Meadow could be a very suitable location for the idealised floodplain woodland restoration outlined by Peterken and Hughes (1995, Table 7.2 option D), a native woodland developing on a naturally flooding floodplain. However, this site is currently used by the landowners for grazing cattle, similar to many floodplain meadows, and therefore to ensure these natural regeneration approaches are also an economically viable option for landowners, it is important to

incorporate them in incentive-based schemes, such as the Higher Level Stewardship Scheme run by Natural England (Natural England, 2013).

Table 7.2 Options for floodplain forest restoration as outlined by Peterken and Hughes (1995). Options A-D represent the extremes between which intermediate alternatives are possible.

		Forest	
		Managed	***Not Managed***
River	***Managed***	**A:** Plant woodland on a floodplain whose river remains constrained within existing channels	**B:** Establish new native woodland, but leave it to develop naturally. The river remains constrained within existing channels
	Not Managed	**C:** Plant new woodland on a floodplain where the river is allowed to flood and meander without restraint	**D:** Establish new native woodland, but leave it to develop naturally on a floodplain where the river is allowed to flood and meander without restraint

*Figure 7.1 Hunworth Meadow after the removal of river embankments. Photo taken looking north-west in April 2009. While the river was embanked, alder (*Alnus glutinosa*) had been growing in the wetter areas of the floodplain.*

*Figure 7.2 High prominence of alder (*Alnus glutinosa*) saplings growing near the river bank on Hunworth Meadow after the restoration of natural disturbance regimes. Photo taken in June 2013.*

7.3 Conclusions

Concern for the loss of natural floodplain habitats has highlighted the need for a better understanding of the biodiversity of these landscapes and its responses to anthropogenic change. These responses need to be recognised in order to facilitate the effective implementation of conservation and restoration policies. By undertaking an in-depth, comparative biodiversity analysis over multiple scales for two highly diverse beetle families, this thesis has demonstrated that anthropogenic land use changes have had a substantial influence on chalk floodplain beetle communities. Most notably, site management considerably changes community composition and creates distinctly different communities amongst meadow, fen and woodland habitats along the studied chalk rivers in Norfolk. Whereas the conservation of a mosaic of different habitat types of suitable areas is needed to help maintain overall gamma diversity and meta-populations within the middle reaches of these catchments, some specific habitats appear to need particularly urgent attention for conservation strategies. Floodplain woodlands, which harboured species sharing a combination of life traits associated with vulnerability to land use change, and floodplain fens, which hosted uncharacteristically low beetle species numbers and showed evidence of heavy influence from the surrounding landscapes, should be given more attention in current river floodplain restoration and conservation.

There are two main caveats in the use of ground-living beetles for ecological studies. First, pitfall trapping as their standard recording method has been subject to wide criticism due to its reliance on activity, under-sampling of small species and dependence on preservatives (Greenslade, 1964; Luff, 1968; Baars, 1979; Niemalä *et al.*, 1990; Topping & Sunderland, 1992; Spence & Niemelä, 1994; Lang, 2000; Woodcock, 2005). The second is the great amount of data required to identify significant trends and draw statistically appropriate conclusions with such highly diverse taxa. However, the large number of specimens collected in this study, the replications across two years and multiple seasons, and the detailed and specific analysis, which recognised the limitations of pitfall sampling methodologies, enabled strong conclusions to be drawn regarding the anthropogenic influences on beetle communities in chalk floodplains.

It is estimated that about one quarter of all species on earth are beetles (Ødegaard, 2000; Hunt *et al.*, 2007; Hamilton *et al.*, 2010), which play essential roles in the functioning of ecosystems (Bouchard *et al.*, 2009; Schuldt & Assmann, 2010) and in most food webs (e.g. Paetzold *et al.*, 2005; Hagar *et al.*, 2012). While this study of chalk floodplains has contributed to our understanding of beetle diversity and ecology, many more studies are needed; we are only just beginning to understand the actual extent of direct and indirect effects of anthropogenic influences on beetles across the globe.

7.4 Future directions

The combined focus on different aspects of the beetle biodiversity of chalk river floodplains across multiple scales and different families represents an original way to understand the communities in these complex yet threatened ecosystems. In particular, the inclusion of staphylinid beetles provided a greater understanding of these lesser-studied communities within floodplains and revealed the importance of considering multiple taxa responses to micro, local and landscape factors. The following, concluding paragraphs illustrate future directions for research that would further improve our comprehension of the biodiversity within floodplain environments.

Firstly, to fully understand anthropogenic impacts on the biodiversity of chalk river floodplains, palaeoecological techniques could be used to characterise the presence and abundances of different carabid and staphylinid taxonomic and functional groups that inhabited these floodplains in the past. This method has been used for within

stream and floodplain habitats before (e.g. Brown, 1988; Amoros & Van Urk, 1989; Buckland & Dinnin, 1993; Brayshay & Dinnin, 1999; Thoms *et al.*, 1999; Brown, 2002; Davis *et al.*, 2007; Howard *et al.*, 2009; Seddon *et al.*, 2012) with the aim of forming a baseline for informed decisions regarding restoration and management. Within the context of this research, such methods could not only enhance the understanding of changes in species and communities and offer a temporal perspective on anthropogenic influences, but also provide a means of establishing baseline reference conditions for restoration (Thoms *et al.*, 1999; Davis *et al.*, 2007).

Secondly, while the study of current assemblages of 15 floodplain sites enabled an understanding of the beetle species occupying these habitats, incorporating other catchments with different geological parent materials could permit additional understanding of the uniqueness of chalk floodplains. This could accordingly inform specific conservation policies targeted specifically at chalk rivers and floodplains, such as the UK government's Biodiversity Action Plans for Chalk River Habitats (Maddock, 2008).

Thirdly, this study revealed the importance of habitat area on floodplain beetle assemblages. Further research is needed to ascertain whether optimal areas exist in these environments to support the persistence of habitat-specific species and communities, and in particular communities with sets of vulnerable functional traits.

Fourthly, while the scale of this study and the number of specimens collected were well suited to the scope of a PhD thesis, additional beetle collection methods have been shown to effectively supplement pitfall trapping (Duelli & Obrist, 1998; Lassau *et al.*, 2005; Hyvarinen *et al.*, 2006; Liu *et al.*, 2007; Billeter *et al.*, 2008). Methods such as active collection, light trapping and flight interception traps may enhance the understanding of beetle assemblages within these floodplains. In the sampling of Alder Carr on the River Wissey, a flight interception trap was set up collectively with the Norfolk Recorder, Martin Collier, to obtain a full year dataset of Coleoptera within this floodplain forest. Analysis of these samples may reveal more about the general communities found within this floodplain and supplement the findings of this thesis.

Finally, further research is needed to increase the staphylinid beetle research base in general. Carabids have long been the focus of ecological research (Rainio & Niemelä, 2003), whilst literature on staphylinid morphology, ecology and response to anthropogenic and environmental gradients is evidently lacking. For example, an extensive literature review revealed information on the functional traits of a select

number of staphylinid species, yet no information was available on the majority of the species encountered in this study. Increased understanding of these often highly specialised species could enhance our knowledge of the biodiversity in a multitude of habitats since staphylinid beetles are present in almost all terrestrial environments in the UK, and could help drive forward the science of coleopterology.

References

Acreman, M., Fisher, J., Stratford, C., Mould, D. & Mountford, J. (2007) Hydrological science and wetland restoration: some case studies from Europe. *Hydrology and Earth System Sciences*, **11**, 158-169.

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos*, **49**, 340-346.

Adis, J. & Junk, W.J. (2002) Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. *Freshwater Biology*, **47**, 711-731.

Akçakaya, H.R., Mills, G. & Doncaster, C.P. (2007) The role of metapopulations in conservation. *Key Topics in Conservation Biology* (ed. by D. Macdonald and K. Service), pp. 64-84. Blackwell Publishing, Oxford.

Alaruikka, D., Kotze, D.J., Matveinen, K. & Niemelä, J. (2002) Carabid beetle and spider assemblages along a forested urban–rural gradient in southern Finland. *Journal of Insect Conservation*, **6**, 195-206.

Amoros, C. & Van Urk, G. (1989) Palaeoecological analysis of large rivers: some principles and methods. *Historical Change of Large Alluvial Rivers* (ed. by G. Petts, H. Moller and A. Roux), pp. 143-166. Wiley, Chichester.

Ander, E.L., Shand, P. & Wood, S. (2006) *Baseline Report Series: 21. The Chalk and Crag of north Norfolk and the Waveney catchment. British Geological Survey Commissioned Report No. CR/06/043N*. Environment Agency, Solihull.

Andersen, J. (1983) The habitat distribution of species of the tribe Bembidiini (Coleoptera, Carabidae) on banks and shores in northern Norway. *Notulae Entomologicae*, **63**, 131-142.

Andersen, J. & Hanssen, O. (2005) Riparian beetles, a unique, but vulnerable element in the fauna of Fennoscandia. *Biodiversity & Conservation*, **14**, 3497-3524.

Anderson, M. & Cribble, N. (1998) Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Australian Journal of Ecology*, **23**, 158-167.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32-46.

Anderson, M.J. (2005) *PERMANOVA: Permutational multivariate analysis of variance: a computer program*. Department of Statistics, University of Auckland, New Zealand.

Anderson, M.J. (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, **62**, 245-253.

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, **84**, 511-525.

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, **9**, 683-693.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S. & Davies, K.F. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19-28.

Anderson, R. (1997) *Rove Beetles (Coleoptera: Staphylinidae)*. Environment Agency, Northern Ireland.

Antvogel, H. & Bonn, A. (2001) Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography*, **24**, 470-482.

Apigian, K.O., Dahlsten, D.L. & Stephens, S.L. (2006) Biodiversity of Coleoptera and the importance of habitat structural features in a Sierra Nevada mixed-conifer forest. *Environmental Entomology*, **35**, 964-975.

Assmann, T. (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). *Biodiversity & Conservation*, **8**, 1499-1517.

Aviron, S., Burel, F., Baudry, J. & Schermann, N. (2005) Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agriculture, Ecosystems & Environment*, **108**, 205-217.

Axmacher, J., Kühne, L. & Vohland, K. (2008) Notes on α-and β-diversity pattern of selected moth families. *Butterflies and Moth Diversity of the Kakamega Forest (Kenya)* (ed. by L. Kühne), pp. 35-46. Brandenburgische University, Germany.

Axmacher, J., Tünte, H., Schrumpf, M., Müller-Hohenstein, K., Lyaruu, H. & Fiedler, K. (2004a) Diverging diversity patterns of vascular plants and geometrid moths during forest regeneration on Mt Kilimanjaro, Tanzania. *Journal of Biogeography*, **31**, 895-904.

Axmacher, J.C., Liu, Y., Wang, C., Li, L. & Yu, Z. (2011) Spatial α-diversity patterns of diverse insect taxa in Northern China: lessons for biodiversity conservation. *Biological Conservation*, **144**, 2362-2368.

Axmacher, J.C., Holtmann, G., Scheuermann, L., Brehm, G., Müller Hohenstein, K. & Fiedler, K. (2004b) Diversity of geometrid moths (Lepidoptera: Geometridae) along an afrotropical elevational rainforest transect. *Diversity and Distributions*, **10**, 293-302.

Axmacher, J.C., Brehm, G., Hemp, A., Tünte, H., Lyaruu, H.V.M., Müller-Hohenstein, K. & Fiedler, K. (2009) Determinants of diversity in afrotropical herbivorous insects

(Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *Journal of Biogeography*, **36**, 337-349.

Baars, M. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia*, **41**, 25-46.

Bailey, A.D. (1998) Floodplains and agriculture. *United Kingdom Floodplains* (ed. by R.G. Bailey, P.V. José and B.R. Sherwood), pp. 11-15. Westbury, Yorkshire.

Bailey, J. (2007) *Death by dredging! Fish and Fly Online*. Available at: http://www.flyforums.co.uk/news/flyfishing/features/fishinguk/5033.html (accessed 3 August 2011).

Baiocchi, S., Fattorini, S., Bonavita, P. & Taglianti, A.V. (2012) Patterns of beta diversity in riparian ground beetle assemblages (Coleoptera Carabidae): a case study in the River Aniene (Central Italy). *Italian Journal of Zoology*, **79**, 136-150.

Baker, R. & Lambley, P. (1983) The River Glaven. *Transactions of the Norfolk and Norwich Naturalist Society*, **26**, 173-183.

Bakker, J.P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*, **14**, 63-68.

Ballinger, A., Lake, P. & Nally, R.M. (2007) Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. *Oecologia*, **152**, 227-238.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146-1156.

Barbaro, L. & Van Halder, I. (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography*, **32**, 321-333.

Barber, K.R., Leeds-Harrison, P.B., Lawson, C.S. & Gowing, D.J.G. (2004) Soil aeration status in a lowland wet grassland. *Hydrological Processes*, **18**, 329-341.

Barton, P.S., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Cunningham, S.A. (2009) Conserving ground-dwelling beetles in an endangered woodland community: multi-scale habitat effects on assemblage diversity. *Biological Conservation*, **142**, 1701-1709.

Barton, P.S., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Cunningham, S.A. (2010) Fine-scale heterogeneity in beetle assemblages under co-occurring Eucalyptus in the same subgenus. *Journal of Biogeography*, **37**, 1927-1937.

Barton, P.S., Gibb, H., Manning, A.D., Lindenmayer, D.B. & Cunningham, S.A. (2011a) Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. *Biological Journal of the Linnean Society*, **102**, 301-310.

Barton, P.S., Manning, A.D., Gibb, H., Wood, J.T., Lindenmayer, D.B. & Cunningham, S.A. (2011b) Experimental reduction of native vertebrate grazing and addition of logs benefit beetle diversity at multiple scales. *Journal of Applied Ecology*, **48**, 943-951.

Batáry, P., Báldi, A., Szél, G., Podlussány, A., Rozner, I. & Erdős, S. (2007) Responses of grassland specialist and generalist beetles to management and landscape complexity. *Diversity and Distributions*, **13**, 196-202.

Bates, A.J., Sadler, J.P., Perry, J.N. & Fowles, A.P. (2007) The microspatial distribution of beetles (Coleoptera) on exposed riverine sediments (ERS). *European Journal of Entomology*, **104**, 479.

Bauer, L.J. (1989) Moorland beetle communities on limestone `Habitat Islands'. II. Flight activity, and its influence on local staphylinid diversity. *Journal of Animal Ecology*, **58**, 1099-1113.

Bauer, T. (1981) Prey capture and structure of the visual space of an insect that hunts by sight on the litter layer (*Notiophilus biguttatus* F., Carabidae, Coleoptera). *Behavioral Ecology and Sociobiology*, **8**, 91-97.

Bauer, T. & Kredler, M. (1993) Morphology of the compound eyes as an indicator of life-style in carabid beetles. *Canadian Journal of Zoology*, **71**, 799-810.

Beck, J., Pfiffner, L., Ballesteros-Mejia, L., Blick, T. & Luka, H. (2013) Revisiting the indicator problem: can three epigean arthropod taxa inform about each other's biodiversity? *Diversity and Distributions*, **19**, 688–699.

Beebe, W. (1996) It's a beetles life. *An Inordinate Fondness for Beetles* (ed. by A.V. Evans and C.L. Bellamy), pp. 94-135. University of California Press, Berkeley.

Bengtsson, J. (1998) Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Applied Soil Ecology*, **10**, 191-199.

Bengtsson, J., Nilsson, S.G., Franc, A. & Menozzi, P. (2000) Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, **132**, 39-50.

Benstead, B., Drake, M., José, P., Mountford, O., Newbold, C. & Treweek, J. (1997) *The Wet Grassland Guide*. RSPB, Bedforshire.

Berg, D.R., McKee, A. & Maki, M.J. (2003) Restoring floodplain forests. *Restoration of Puget Sound Rivers* (ed. by D.R. Montgomery, S. Bolton, D.B. Booth and L. Wall), pp. 248-291. University of Washington Press, Seattle, Washington.

Bernhardt, E.S., Palmer, M., Allan, J., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C. & Follstad-Shah, J. (2005) Synthesizing US river restoration efforts. *Science*, **308**, 636.

Bernhardt, E.S., Sudduth, E.B., Palmer, M.A., Allan, J.D., Meyer, J.L., Alexander, G., Follastad Shah, J., Hassett, B., Jenkinson, R. & Lave, R. (2007) Restoring rivers one reach at a time: results from a survey of US river restoration practitioners. *Restoration Ecology*, **15**, 482-493.

Bettacchioli, G., Taormina, M., Bernini, F. & Migliorini, M. (2012) Disturbance regimes in a wetland remnant: implications for trait-displacements and shifts in the assemblage structure of carabid beetles (Coleoptera: Carabidae). *Journal of Insect Conservation*, **16**, 249-261.

Betz, O. (1999) A behavioural inventory of adult *Stenus* species (Coleoptera: Staphylinidae). *Journal of Natural History*, **33**, 1691-1712.

Betz, O. (2002) Performance and adaptive value of tarsal morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae). *Journal of Experimental Biology*, **205**, 1097.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R. & Burel, F. (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology*, **45**, 141-150.

Bischoff, A. (2002) Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biological Conservation*, **104**, 25-33.

Bissels, S., Holzel, N., Donath, T.W. & Otte, A. (2004) Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biological Conservation*, **118**, 641-650.

Blackstock, T., Rimes, C., Stevens, D., Jefferson, R., Robertson, H., Mackintosh, J. & Hopkins, J. (1999) The extent of semi-natural grassland communities in lowland England and Wales: a review of conservation surveys 1978-96. *Grass and Forage Science*, **54**, 1-18.

Blair, A. (2006) *The River Great Ouse and Tributaries*. Imray Laurie Norie and Wilson Ltd, St Ives, Cambridgeshire.

Blake, S., Foster, G., Eyre, M.D. & Luff, M.L. (1994) Effects of habitat type and grassland management practices on body size distribution of carabid beetles. *Pedobiologia*, **38**, 502-512.

Blake, S., McCracken, D.I., Eyre, M.D., Garside, A. & Foster, G.N. (2003) The relationship between the classification of Scottish ground beetle assemblages (Coleoptera, Carabidae) and the National Vegetation Classification of British plant communities. *Ecography*, **26**, 602-616.

Bohac, J. (1999) Staphylinid beetles as bioindicators. *Agriculture, Ecosystems & Environment*, **74**, 357-372.

Boháč, J., Matějíček, J. & Rous, R. (2007) Check-list of staphylinid beetles (Coleoptera, Staphylinidae) of the Czech Republic and the division of species according to their ecological characteristics and sensitivity to human influence. *Časopis Slezského Muzea Opava (A)*, **56**, 227-276.

Bonar, S., Fehmi, J. & Mercado-Silva, N. (2011) An overview of sampling issues in species diversity and abundance surveys. *Biological Diversity: Frontiers in Measurement and Assessment* (ed. by A.E. Magurran and B.J. Mcgill), pp. 11-24. Oxford University Press, Oxford.

Bonn, A. & Kleinwächter, M. (1999) Microhabitat distribution of spider and ground beetle assemblages (Araneae, Carabidae) on frequently inundated river banks of the River Elbe. *Zeitschrift für Ökologie und Naturschutz*, **8**, 109-124.

Bonn, A., Hagen, K. & Reiche, D.W. (2002) The significance of flood regimes for carabid beetle and spider communities in riparian habitats - a comparison of three major rivers in Germany. *River Research and Applications*, **18**, 43-64.

Bonnet, X., Shine, R. & Lourdais, O. (2002) Taxonomic chauvinism. *Trends in Ecology & Evolution*, **17**, 1-3.

Borcard, D. & Legendre, P. (1994) Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environmental and Ecological Statistics*, **1**, 37-61.

Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51-68.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045-1055.

Borges, P.A.V. & Brown, V.K. (2003) Estimating species richness of arthropods in Azorean pastures: the adequacy of suction sampling and pitfall trapping. *Graellsia*, **59**, 7-24.

Boscaini, A., Franceschini, A. & Maiolini, B. (2000) River ecotones: carabid beetles as a tool for quality assessment. *Hydrobiologia*, **422**, 173-181.

Bouchard, P., Grebennikov, V.V., Smith, A.B.T. & Douglas, H. (2009) Biodiversity of Coleoptera. *Insect Biodiversity: Science and Society* (ed. by R.G. Foottit and P.H. Adler), pp. 265-301. Wiley, Oxford.

Bozdogan, H. (1987) Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. *Psychometrika*, **52**, 345-370.

Brayshay, B.A. & Dinnin, M. (1999) Integrated palaeoecological evidence for biodiversity at the floodplain-forest margin. *Journal of Biogeography*, **26**, 115-131.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brodie, J. (1985) Vegetation asnalysis. *Grassland Studies* (ed. by J. Brodie), pp. 7-9. George Allen and Unwin, Boston, MA.

Brookes, A. (1988) *Channelized Rivers: Perspectives for Environmental Management*. John Wiley & Sons, Chichester.

Brookes, A. & Shields, F.D. (1996) *River channel restoration: guiding principles for sustainable projects*. John Wiley & Sons.

Brooks, D., Bater, J., Clark, S., Monteith, D., Andrews, C., Corbett, S., Beaumont, D. & Chapman, J. (2012) Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, **49**, 1009-1019.

Brooks, J.L. & Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28-35.

Brose, U. (2002) Estimating species richness of pitfall catches by non-parametric estimators. *Pedobiologia*, **46**, 101-107.

Brose, U. (2003a) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, **135**, 407-413.

Brose, U. (2003b) Regional diversity of temporary wetland carabid beetle communities: a matter of landscape features or cultivation intensity? *Agriculture, Ecosystems & Environment*, **98**, 163-167.

Brose, U. & Martinez, D.N. (2004) Estimating the richness of species with variable mobility. *Oikos*, **105**, 292-300.

Brown, A. (1988) The palaeoecology of Alnus (alder) and the postglacial history of floodplain vegetation. Pollen percentage and influx data from the West Midlands, United Kingdom. *New Phytologist*, **110**, 425-436.

Brown, A. (1997) Biogeomorphology and diversity in multiple-channel river systems. *Global Ecology and Biogeography Letters*, **6**, 179-185.

Brown, A. (2002) Learning from the past: palaeohydrology and palaeoecology. *Freshwater Biology*, **47**, 817-829.

Buckland, P. & Dinnin, M. (1993) Holocene woodlands, the fossil evidence. *Dead Wood Matters: the Ecology and Conservation of Saproxylic Invertebrates in Britain* (ed. by K. Kirby and C. Drake), pp. 6-20. English Nature, Peterborough, England.

Buckland, S., Magurran, A., Green, R. & Fewster, R. (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 243-254.

Buijse, A.D., Coops, H., Staras, M., Jans, L.H., Van Geest, G.J., Grift, R.E., Ibelings, B.W., Oosterberg, W. & Roozen, F.C.J.M. (2002) Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology*, **47**, 889-907.

Burel, F. (1989) Landscape structure effects on carabid beetles spatial patterns in western France. *Landscape Ecology*, **2**, 215-226.

Burke, D. & Goulet, H. (1998) Landscape and area effects on beetle assemblages in Ontario. *Ecography*, **21**, 472-479.

Burnham, K.P. & Overton, W.S. (1978) Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika*, **65**, 625-633.

Burnham, K.P. & Overton, W.S. (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology*, **60**, 927-936.

Buse, A. & Good, J.E.G. (1993) The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): implications for conservation. *Biological Conservation*, **64**, 67-76.

Cadotte, M.W. (2011) The new diversity: management gains through insights into the functional diversity of communities. *Journal of Applied Ecology*, **48**, 1067-1069.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E. & Hobbie, S.E. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234-242.

Chatters, C. (2013) Is tree planting good for wildlife? *British Wildlife*, **24**, 162-166.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clarke, S.J., Bruce-Burgess, L. & Wharton, G. (2003) Linking form and function: towards an eco hydromorphic approach to sustainable river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**, 439-450.

Clilverd, H., Thompson, J., Heppell, C., Sayer, C. & Axmacher, J. (2013) River–floodplain hydrology of an embanked lowland Chalk river and initial response to embankment removal. *Hydrological Sciences Journal*, **58**, 627-650.

Clough, Y., Kruess, A. & Tscharntke, T. (2007) Organic versus conventional arable farming systems: Functional grouping helps understand staphylinid response. *Agriculture, Ecosystems & Environment*, **118**, 285-290.

Cole, L.J., McCracken, D.I., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy, K.J. & Waterhouse, T. (2002) Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. *Agriculture, Ecosystems & Environment*, **93**, 323-336.

Colwell, R.K. (2009) *EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2.* Available at: http://purl.oclc.org/estimates. (accessed 8 August 2012).

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **345**, 101-118.

Cook, W.M., Lane, K.T., Foster, B.L. & Holt, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619-623.

Cooter, J. & Barcley, M.V.L.(eds.) (2006) *A Coleopterist's Handbook*, 4th edn. The Amateur Entomologists' Society, Kent, England.

Coscaron, M., Melo, M., Coddington, J. & Corronca, J. (2009) Estimating biodiversity: a case study on true bugs in Argentinian wetlands. *Biodiversity & Conservation*, **18**, 1491-1507.

Crist, T.O. & Wiens, J.A. (1995) Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). *Journal of Animal Ecology*, **64**, 733-746.

Da Silva, P.M., Aguiar, C.A., Niemelä, J., Sousa, J.P. & Serrano, A.R. (2008) Diversity patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use disturbance. *Agriculture, Ecosystems & Environment*, **124**, 270-274.

Daily, G.C. (1995) Restoring value to the world's degraded lands. *Science*, **269**, 350-354.

Dauber, J., Purtauf, T., Allspach, A., Frisch, J., Voigtländer, K. & Wolters, V. (2005) Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. *Global Ecology and Biogeography*, **14**, 213-221.

Davies, K.F., Margules, C.R. & Lawrence, J.F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**, 1450-1461.

Davis, M.A. (2000) " Restoration"--A Misnomer? *Science*, **287**, 1203.

Davis, S., Brown, A. & Dinnin, M. (2007) Floodplain connectivity, disturbance and change: a palaeoentomological investigation of floodplain ecology from south-west England. *Journal of Animal Ecology*, **76**, 276-288.

De Cáceres, M. (2013) *How to use the indicspecies package (ver. 1.6. 7)*. Available at: http://cran.rproject.org/web/packages/indicspecies/vignettes/indicspeciesTutorial.pdf (accessed 2 April 2013).

De Cáceres, M. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, **90**, 3566-3574.

De Cáceres, M., Legendre, P. & Moretti, M. (2010) Improving indicator species analysis by combining groups of sites. *Oikos*, **119**, 1674-1684.

De La Peña, N.M., Butet, A., Delettre, Y., Morant, P. & Burel, F. (2003) Landscape context and carabid beetles (Coleoptera: Carabidae) communities of hedgerows in western France. *Agriculture, Ecosystems & Environment*, **94**, 59-72.

De Vries, H., Den Boer, P. & Van Dijk, T.S. (1996) Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia*, **107**, 332-342.

Deakin, R. (1999) *Waterlog: a Swimmer's Journey through Britain*. Vintage Books, London.

Dean, W.E. (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. *Journal of Sedimentary Research*, **44**, 242-248.

DEFRA (1994) *Biodiversity: The UK Action Plan*. HMSO, London.

DEFRA (2007) *England Catchment Sensitive Farming Initiative: List of Priority Catchments*. DEFRA, London.

Den Boer, P. (1977) *Dispersal power and survival: carabids in a cultivated countryside*. H. Veenman & Zonen B.V., Wageningen, Netherlands.

Den Boer, P. (1990a) The survival value of dispersal in terrestrial arthropods. *Biological Conservation*, **54**, 175-192.

Den Boer, P. (1990b) Density limits and survival of local populations in 64 carabid species with different powers of dispersal. *Journal of Evolutionary Biology*, **3**, 19-48.

Dennis, P. (1989) *The Predatory Potential of Staphylinid Beetles in Cereals*. PhD Thesis, University of Southampton.

Dennis, P. & Wratten, S.D. (1991) Field manipulation of populations of individual staphylinid species in cereals and their impact on aphid populations. *Ecological Entomology*, **16**, 17-24.

Dennis, P. & Sotherton, N. (1994) Behavioural aspects of staphylinid beetles that limit their aphid feeding potential in cereal crops. *Pedobiologia*, **38**, 222-237.

Dennis, P., Aspinall, R.J. & Gordon, I.J. (2002) Spatial distribution of upland beetles in relation to landform, vegetation and grazing management. *Basic and Applied Ecology*, **3**, 183-193.

Dennis, P., Young, M.R., Howard, C.L. & Gordon, I.J. (1997) The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. *Journal of Applied Ecology*, 433-443.

Desender, K. (1989) Ecomorphological adaptations of riparian carabid beetles. *Proceedings of Invertebres de Belgique, Bruxelles (Belgium), 25-26 Nov 1988.* pp. 309-314. Institut Royal des Sciences Naturelles de Belgique, Belgium.

Desender, K., Dufrêne, M. & Maelfait, J.P. (1994) Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a database covering more than a century. *Carabid Beetles: Ecology and Evolution* (ed. by K. Desender, M. Dufrêne, M. Loreau, M.L. Luff and J.P. Maelfait), pp. 247-252. Springer, Netherlands.

Diamond, J. (1984) "Normal" extinctions of isolated populations. *Extinctions* (ed. by M. Nitecki), pp. 191-246. University of Chicago Press, Chicago.

Diamond, J. (1989) Overview of recent extinctions. *Conservation for the Twenty-First Century* (ed. by D. Western and M. Pearl), pp. 37-41. Oxford University Press, Oxford.

Diaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646-655.

Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684-20689.

Díaz, S., Tilman, D., Fargione, J., Chapin III, F., Dirzo, R., Kitzberger, T., Gemmill, B., Zobel, M., Vila, M. & Mitchell, C. (2005) Biodiversity regulation of ecosystem services. *Ecosystems and Human Well-Being: Current State and Trends* (ed. by R.M. Hassan, R. Scholes and N. Ash), pp. 297-329. Island Press, Washington.

Diekotter, T., Billeter, R. & Crist, T.O. (2008) Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. *Basic and Applied Ecology*, **9**, 298-307.

Donath, T.W., Holzel, N. & Otte, A. (2003) The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Applied Vegetation Science*, **6**, 13-22.

Drake, C. (1998) The important habitats and characteristic rare invertebrates of lowland wet grassland in England. *European Floodplain and Coastal Wet Grasslands: Biodiversity, Management and Restoration* (ed. by C. Joyce and P. Wade). John Wiley, Chichester.

Drake, C. & Sheppard, D. (1998) Changes in the fortunes of invertebrates of floodplain habitats. *United Kingdom Floodplains* (ed. by A.D. Bailey, P.V. Jose and B.R. Sherwood), pp. 229-236. Westbury, Yorkshire.

Driscoll, D.A. & Weir, T.O.M. (2005) Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology*, **19**, 182-194.

Duelli, P. & Obrist, M. (1998) In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity & Conservation*, **7**, 297-309.

Duelli, P., Studer, M. & Katz, E. (1990) Minimalprogramme für die Erhebung und Aufbereitung zooökologischer Daten als Fachbeiträge zu Planungen am Beispiel ausgewählter Arthropodengruppen. *Schriftenreine für Landschaftspflege und Naturschutz*, **32**, 211-222.

Duelli, P., Obrist, M.K. & Schmatz, D.R. (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems & Environment*, **74**, 33-64.

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345-366.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, 169-175.

Dutilleul, P., Stockwell, J.D., Frigon, D. & Legendre, P. (2000) The Mantel test versus Pearson's correlation analysis: assessment of the differences for biological and environmental studies. *Journal of Agricultural, Biological, and Environmental Statistics*, 131-150.

EDINA (2012) *Digimap Ordance Survey Service*. Available at: http://edina.ac.uk/digimap (accessed 11 November 2012).

Efron, B. (1979) Bootstrap methods: another look at the jackknife. *The Annals of Statistics*, **7**, 1-26.

Ehrenfeld, J.G. (2000) Defining the limits of restoration: the need for realistic goals. *Restoration Ecology*, **8**, 2-9.

Ehrlich, P.R. & Wilson, E. (1991) Biodiversity studies: science and policy. *Science*, **253**, 758.

Ehrlich, P.R. & Ehrlich, A.H. (1992) The value of biodiversity. *Ambio*, **21**, 219-226.

Ellenberg, H. (1988) *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge.

England Field Unit & Nature Conservancy Council (1990) *Handbook for Phase I Habitat Survey- a Technique for Environmental Audit*. Nature Conservancy Council, Peterborough.

English Nature (2005a) *Norfolk Biodiversity Action Plan, Habitat Action Plan 7: Coastal and Floodplain Grazing Marsh*. English Nature, Norwich.

English Nature (2005b) *Norfolk Biodiversity Action Plan, Habitat Action Plan 4: Fens*. English Nature, Norwich.

Environment Agency (2004) *The State of England's Chalk Rivers.* Environment Agency, Bristol.

Environment Agency (2005) *The North Norfolk Catchment Abstraction Management Strategy*. Environment Agency, Ipswich.

Ewers, R.M. & Didham, R.K. (2006) Continuous response functions for quantifying the strength of edge effects. *Journal of Applied Ecology*, **43**, 527-536.

Ewers, R.M. & Didham, R.K. (2007) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117-142.

Ewers, R.M. & Didham, R.K. (2008) Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences*, **105**, 5426.

Ewers, R.M., Thorpe, S. & Didham, R.K. (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology*, **88**, 96-106.

Eyre, M., Lott, D. & Luff, M. (2001a) The rove beetles (Coleoptera, Staphylinidae) of exposed riverine sediments in Scotland and northern England: habitat classification and conservation aspects. *Journal of Insect Conservation*, **5**, 173-186.

Eyre, M., Luff, M. & Phillips, D. (2001b) The ground beetles (Coleoptera: Carabidae) of exposed riverine sediments in Scotland and northern England. *Biodiversity & Conservation*, **10**, 403-426.

Facelli, J.M. & Pickett, S.T. (1991) Plant litter: light interception and effects on an old-field plant community. *Ecology*, 1024-1031.

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65-74.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 487-515.

Farrell, B.D. (1998) "Inordinate Fondness" explained: why are there So many beetles? *Science*, **281**, 555-9.

Firle, S., Bommarco, R., Ekbom, B. & Natiello, M. (1998) The influence of movement and resting behavior on the range of three carabid beetles. *Ecology*, **79**, 2113-2122.

Fisher, R.A., Corbet, A.S. & Williams, C. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*, **12**, 42-58.

Fojt, W. (1994) Dehydration and the threat to East Anglian fens, England. *Biological Conservation*, **69**, 163-175.

Foord, S., Mafadza, M., Dippenaar-Schoeman, A.S. & Van Rensburg, B.J. (2008) Micro-scale heterogeneity of spiders (Arachnida: Araneae) in the Soutpansberg, South Africa: a comparative survey and inventory in representative habitats. *African Zoology*, **43**, 156-174.

Forestry Commission (2003) *The Management of Semi-Natural Woodlands: Wet Woodlands*. Forestry Commission, Edinburgh.

Forman, R.T.T. (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.

Fournier, E. & Loreau, M. (2001) Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. *Landscape Ecology*, **16**, 17-32.

Frank, J. (1968) The larva and biology of *Quedius picipes* (Mann.) and notes on the biology of five other *Quedius* species (Col., Staphylinidae). *Entomology Monthly Mag*, **104**, 263-268.

Frank, T. & Reichhart, B. (2004) Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. *Bulletin of Entomological Research*, **94**, 209-217.

Fuller, R.M. (1987) The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–1984. *Biological Conservation*, **40**, 281-300.

Gallagher, E.D. (1998) *Compah96 Documentation*. Available at: http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm (accessed 12 September 2012).

Gardiner, J. (1998) Floodplain management in the United Kingdom. *United Kingdom Floodplains* (ed. by R.G. Bailey, P.V. José and B.R. Sherwood), pp. 17-26. Westbury, Yorkshire.

Gardner, S.M. (1991) Ground beetle (Coleoptera: Carabidae) communities on upland heath and their association with heathland flora. *Journal of Biogeography*, 281-289.

Gaston, K.J. (1996) *Biodiversity: a Biology of Numbers and Difference*. Blackwell, Oxford.

Gaublomme, E., Hendrickx, F., Dhuyvetter, H. & Desender, K. (2008) The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. *Biological Conservation*, **141**, 2585-2596.

Gerhard, M. & Reich, M. (2000) Restoration of streams with large wood: effects of accumulated and built-in wood on channel morphology, habitat diversity and aquatic fauna. *International Review of Hydrobiology*, **85**, 123-137.

Gerisch, M. (2011) Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles. *ZooKeys*, **100**, 353-370.

Gerisch, M., Agostinelli, V., Henle, K. & Dziock, F. (2012) More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos*, **121**, 508-515.

Gerisch, M., Schanowski, A., Figura, W., Gerken, B., Dziock, F. & Hanle, K. (2006) Carabid beetles (Coleoptera, Carabidae) as indicators of hydrological site conditions in floodplain grasslands. *International Reviews of Hydrobiologia*, **91**, 326-340.

Ghullam, M. & Ellis, R.W. (2006) *A Botanical Survey of the Meadows, River and Woodland of the Bure Floodplain between Blickling Mill and Ingworth Bridge*. Report for the National Trust, Norfolk.

Gibb, H. & Cunningham, S. (2010) Revegetation of farmland restores function and composition of epigaeic beetle assemblages. *Biological Conservation*, **143**, 677-687.

Giller, P.S. & O'Donovan, G. (2002) Biodiversity and ecosystem function: do species matter? *Biology & Environment: Proceedings of the Royal Irish Academy*, **102**, 129-139.

Gioria, M., Bacaro, G. & Feehan, J. (2011) Evaluating and interpreting cross-taxon congruence: Potential pitfalls and solutions. *Acta Oecologica*, **37**, 187-194.

Gitay, H. & Noble, I.R. (1997) What are functional types and how should we seek them? *Plant Functional Types - Their Relevance to Ecosystem Properties and Global Change* (ed. by T.M. Smith, H.H. Shugart and F.I. Woodward), pp. 3-19. Cambridge University Press, Cambridge.

Glesne, R.S. (1998) *Terrestrial Riparian Arthropod Investigations in the Big Beaver Creek Research Natural Area, North Cascades National Park Service Complex, 1995-1996: Part II Coleoptera*. North Cascades National Park Service Complex, Washington.

Gobbi, M. & Fontaneto, D. (2008) Biodiversity of ground beetles (Coleoptera: Carabidae) in different habitats of the Italian Po lowland. *Agriculture, Ecosystems & Environment*, **127**, 273-276.

Golden, D.M. & Crist, T.O. (2000) Experimental effects of habitat fragmentation on rove beetles and ants: patch area or edge? *Oikos*, **90**, 525-538.

González-Megías, A., María Gómez, J. & Sánchez-Piñero, F. (2007) Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography*, **30**, 31-41.

González-Megías, A., Gómez, J.M. & Sánchez-Piñero, F. (2008) Factors determining beetle richness and composition along an altitudinal gradient in the high mountains of the Sierra Nevada National Park (Spain). *Ecoscience*, **15**, 429-441.

Good, J. & Giller, P. (1991) The effect of cereal and grass management on staphylinid (Coleoptera) assemblages in south-west Ireland. *Journal of Applied Ecology*, **28**, 810-826.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Gotelli, N.J. & Colwell, R.K. (2011) Esimating species richness. *Biological Diversity: Frontiers in Measurement and Assessment* (ed. by B.J. Mcgill and A.E. Magurran), pp. 39-54. Oxford University Press, Oxford.

Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics*, **27**, 857-871.

Gowing, D.J.G. & Spoor, G. (1998) The effect of water table depth on the distribution of plant species on lowland wet grassland. *United Kingdom Floodplains* (ed. by R.G. Bailey, P.V. José and B.R. Sherwood), pp. 185-196. Westbury West Yorkshire.

Gowing, D.J.G., Tallowin, J.R.B., Dise, N.B., Goodyear, J., Dodd, M.E. & Lodge, R.J. (2002) *A Review of the Ecology, Hydrology and Nutrient Dynamics of Floodplain Meadows in England*. English Nature Research Reports No 446, Peterborough.

Grafius, E. & Warner, F. (1989) Predation by *Bembidion quadrimaculatum* (Coleoptera: Carabidae) on *Delia antiqua* (Diptera: Anthomyiidae). *Environmental Entomology*, **18**, 1056-1059.

Grandchamp, A.-C., Bergamini, A., Stofer, S., Niemelä, J., Duelli, P. & Scheidegger, C. (2005) The influence of grassland management on ground beetles (Carabidae, Coleoptera) in Swiss montane meadows. *Agriculture, Ecosystems & Environment*, **110**, 307-317.

Greenslade, P.J.M. (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, **33**, 301-310.

Greenwood, M., Bickerton, M.A., Castella, E., Large, A.R.G. & Petts, G.E. (1991) The use of Coleoptera (Arthropoda: Insecta) for floodplain characterisation on the River Trent, UK. *Regulated Rivers: Research & Management*, **6**, 321-332.

Grevilliot, F., Krebs, L. & Muller, S. (1998) Comparative importance and interference of hydrological conditions and soil nutrient gradients in floristic biodiversity in flood meadows. *Biodiversity & Conservation*, **7**, 1495-1520.

Griffiths, G.J.K., Winder, L., Holland, J.M., Thomas, C. & Williams, E. (2007) The representation and functional composition of carabid and staphylinid beetles in different field boundary types at a farm-scale. *Biological Conservation*, **135**, 145-152.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*, 2nd edn. John Wiley & Sons, Chichester.

Grove, S.J. & Stork, N.E. (2000) An inordinate fondness for beetles. *Invertebrate Taxonomy*, **14**, 733-739.

Günther, J. & Assmann, T. (2005) Restoration ecology meets carabidology: effects of floodplain restitution on ground beetles (Coleoptera, Carabidae). *Biodiversity & Conservation*, **14**, 1583-1606.

Gutzwiller, K.J. (2002) *Applying Landscape Ecology in Biological Conservation*. Springer, New York.

Hafernik, J., Jr. (1992) Threats to invertebrate biodiversity: implications for conservation strategies. *Conservation Biology* (ed. by P.L. Fiedler and S.K. Jain), pp. 171-195. Chapman & Hall, New York.

Hagar, J.C., Li, J., Sobota, J. & Jenkins, S. (2012) Arthropod prey for riparian associated birds in headwater forests of the Oregon Coast Range. *Forest Ecology and Management*, **285**, 213-226.

Hall, L.S., Krausman, P.R. & Morrison, M.L. (1997) The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin*, **25**, 173-182.

Halme, E. & Niemelä, J. (1993) Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici*, **30**, 17-30.

Hamilton, A.J., Basset, Y., Benke, K.K., Grimbacher, P.S., Miller, S.E., Novotny, V., Samuelson, G.A., Stork, N.E., Weiblen, G.D. & Yen, J.D. (2010) Quantifying uncertainty in estimation of tropical arthropod species richness. *The American Naturalist*, **176**, 90-5.

Hammond, P. (1998) Riparian and floodplain arthropod assemblages: their characteristic and rapid assessment. *United Kingdom Floodplains* (ed. by R.G. Bailey, P.V. José and B.R. Sherwood), pp. 237-282. Westbury, Yorkshire.

Hammond, P. (2003) *Development of Understanding of Habitat Requirements of Invertebrates on Priority Habitats: Staphylindae (including Scaphidiinae and Pselaphinae and Scydmaenidae)*. Buglife, Windsor.

Hammond, P.M. (1974) Changes in the British Coleopterous fauna. *The Chaning Flora and Fauna of Britain* (ed. by D.L. Hawksworth), pp. 323-369. Academic Press, London.

Hammond, P.M. (1996) *A Taxonomic Review of Possible Endemic British Non-Marine Invertebrates*. Unpublished report to English Nature, London.

Harding, J., Benfield, E., Bolstad, P., Helfman, G. & Jones, E. (1998) Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences*, **95**, 14843-14847.

Harper, D., Witkowski, F., Kemp-McCarthy, D. & Crabb, J. (1997) The distribution and abundance of riparian trees in English lowland floodplains. *Global Ecology and Biogeography Letters*, **6**, 297-306.

Harper, D.M., Ebrahimnezhad, M., Taylor, E., Dickinson, S., Decamp, O., Verniers, G. & Balbi, T. (1999) A catchment scale approach to the physical restoration of lowland UK rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **9**, 141-157.

Harper, J.L. & Hawksworth, D.L. (1995) Preface. *Biodiversity: Measurement and Estimation* (ed. by D.L. Hawksworth), pp. 5-12. Chapman & Hall, London.

Harrison, S.S.C. & Harris, I.T. (2002) The effects of bankside management on chalk stream invertebrate communities. *Freshwater Biology*, **47**, 2233-2245.

Hassell, M.P. & Southwood, T. (1978) Foraging strategies of insects. *Annual Review of Ecology and Systematics*, **9**, 75-98.

Heliölä, J., Koivula, M. & Niemelä, J. (2001) Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest–clearcut ecotone. *Conservation Biology*, **15**, 370-377.

Hellawell, J.M. (1988) River regulation and nature conservation. *Regulated Rivers: Research & Management*, **2**, 425-443.

Hellmann, J.J. & Fowler, G.W. (1999) Bias, precision, and accuracy of four measures of species richness. *Ecological Applications*, **9**, 824-834.

Hendrickx, F., Maelfait, J.-P., Wingerden, W.V., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V. & Bugter, R. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, **44**, 340-351.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity & Conservation*, **13**, 207-251.

Hering, D. & Plachter, H. (1997) Riparian ground beetles (Coeloptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. *Oecologia*, **111**, 261-270.

Heuvelmans, M. (1974) *The River Killers*. Stackpole Books, Harrisburg, Pennsylvania.

Hewitt, J., Thrush, S., Lohrer, A. & Townsend, M. (2010) A latent threat to biodiversity: consequences of small-scale heterogeneity loss. *Biodiversity & Conservation*, **19**, 1315-1323.

Hill, M.O. (1973) Diversity and evenness: a unifying notion and its consequences. *Ecology*, **54**, 427-432.

Hinton, H.E. & Stephens, F.L. (1941) Notes on the food of *Micropeplus*, with a description of the pupa of *M. Fulvus* Erichson (Coleoptera: Micropeplidae). *Proceedings of the Royal Entomological Society of London. Series A, General Entomology*, **16**, 29-32.

Hiscock, K., Lister, D., Boar, R. & Green, F. (2001) An integrated assessment of long-term changes in the hydrology of three lowland rivers in eastern England. *Journal of Environmental Management*, **61**, 195-214.

Holland, M., Risser, P.G. & Naiman, R.J.(eds.) (1991) *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*. Chapman & Hall, London.

Holloway, J., Kirk-Spriggs, A. & Khen, C.V. (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **335**, 425-436.

Holopainen, J.K. (1990) Influence of ethylene glycol on the numbers of carabids and other soil arthropods caught in pitfall traps. *The Role of Ground Beetles in Ecological and Environmental Studies* (ed. by N. Stork), pp. 339-341. Intercept, Andover.

Honek, A., Martinkova, Z., Saska, P. & Pekar, S. (2007) Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). *Basic and Applied Ecology*, **8**, 343-353.

Hooper, D., Chapin III, F., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M. & Naeem, S. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.

Howard, A.J., Macklin, M.G. & Passmore, D.G.(eds.) (2003) *Alluvial Archaeology in Europe: Proceedings of the Alluvial Archaeology of NW Europe and the Mediterranean*. Taylor & Francis, London.

Howard, L.C., Wood, P.J., Greenwood, M.T. & Rendell, H.M. (2009) Reconstructing riverine paleo-flow regimes using subfossil insects (Coleoptera and Trichoptera): the application of the LIFE methodology to paleochannel sediments. *Journal of Paleolimnology*, **42**, 453-466.

Hubbard, C.E. (1984) *Grasses: A Guide to their Structure, Identification, Uses, and Distribution in the British Isles*, 3rd edn. Penguin Books, London.

Hughes, F. & Richards, K. (2003) *The Flooded Forest: Guidance for Policy Makers and River Managers in Europe on the Restoration of Floodplain Forests*. FLOBAR2 Project, University of Cambridge, Cambridge.

Hughes, F., Adams, W., Muller, E., Nilsson, C., Richards, K., Barsoum, N., Decamps, H., Foussadier, R., Girel, J. & Guilloy, H. (2001) The importance of different scale processes for the restoration of floodplain woodlands. *Regulated Rivers: Research & Management*, **17**, 325-345.

Hughes, F.M.R. & Rood, S.B. (2001) Floodplains. *Habitat Conservation: Managing the Physical Environment* (ed. by A. Warren and J.R. French), pp. 105-121. John Wiley & Sons, Chichester.

Hunt, T., Bergsten, J., Levkanicova, Z., A Papadopoulou, O.S.J., John, O.S., Wild, R. & Hammond, P.M. (2007) A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, **318**, 1913-1916.

Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 723-732.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145-159.

Hyman, P. & Parsons, M. (1992) *A review of the scarce and threatened Coleoptera of Great Britain Part 1*. Joint Nature Conservation Committee, Peterborough.

Hyvarinen, E., Koukoi, J. & Martikainen, P. (2006) A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *European Journal of Entomology*, **103**, 397-407.

Irmler, U., Arp, H. & Nötzold, R. (2010) Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. *Journal of Insect Conservation*, **14**, 227-235.

Janssen, P., Fortin, D. & Hébert, C. (2009) Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. *Ecography*, **32**, 423-432.

Januschke, K., Brunzel, S., Haase, P. & Hering, D. (2011) Effects of stream restorations on riparian mesohabitats, vegetation and carabid beetles. *Biodiversity & Conservation*, **20**, 3147-3164.

Jeanneret, P., Schüpbach, B. & Luka, H. (2003a) Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. *Agriculture, Ecosystems & Environment*, **98**, 311-320.

Jeanneret, P., Schüpbach, B., Pfiffner, L. & Walter, T. (2003b) Arthropod reaction to landscape and habitat features in agricultural landscapes. *Landscape Ecology*, **18**, 253-263.

Jefferson, R.G. & Grice, P.V. (1998) The conservation of lowland wet grassland in England. *European Wet Grasslands: Biodiversity, Management and Restoration* (ed. by C. Joyce and P.M. Wade), pp. 31-48. John Wiley & Sons, Chichester.

Jermy, A.C., Simpson, D.A., Foley, M.J.Y. & Porter, M.S. (2007) *Sedges of the British Isles BSBI Handbook No 1*, 3rd edn. Botanical Society of the British Isles, London.

Johansson, T. (1999) Site index curves for common alder and grey alder growing on different types of forest soil in Sweden. *Scandinavian journal of forest research*, **14**, 441-453.

Johnson, K.H., Vogt, K.A., Clark, H.J., Schmitz, O.J. & Vogt, D.J. (1996) Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology & Evolution*, **11**, 372-377.

Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S. & Schneider, R.L. (1994) Woody plant regeneration in four floodplain forests. *Ecological Monographs*, **64**, 345-367.

Jongman, R.H., Ter Braak, C.J. & van Tongeren, O.F. (1995) *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge.

Jongman, R.H.G. (2002) Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning*, **58**, 211-221.

Jonsen, I.D. & Fahrig, L. (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology*, **12**, 185-197.

Jost, L. (2006) Entropy and diversity. *Oikos*, **113**, 363-375.

Joy, N.H. (1910) The Behaviour of Coleoptera in time of Floods. *Transactions of the Royal Entomological Society of London*, **58**, 379-385.

Joy, N.H. (1932) *A Practical Handbook of British Beetles*. Witherby, London.

Joyce, C.B. & Wade, P.M.(eds.) (1998) *European Wet grasslands: Biodiversity, Management and Restoration*. John Wiley & Sons Ltd, Chichester.

Junk, W.J. & Welcomme, R.L. (1990) Floodplains. *Wetlands and Shallow Continental Water Bodies* (ed. by B. Patten), pp. 491-542. SPB Academic Publishers, The Hague, Netherlands.

Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, **106**, 110-127.

Kappes, H. & Topp, W. (2004) Emergence of Coleoptera from deadwood in a managed broadleaved forest in central Europe. *Biodiversity & Conservation*, **13**, 1905-1924.

Kasule, F. (1968) Field studies on the life-histories of some British Staphylinidae (Coleoptera). *Transactions of the Society for British Entomology*, **18**, 49-80.

Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157-164.

Kempton, R. & Wedderburn, R. (1978) A comparison of three measures of species diversity. *Biometrics*, **34**, 25-37.

Kempton, R.A. & Taylor, L.R. (1974) Log-series and log-normal parameters as diversity determinants for the Lepidoptera. *Journal of Animal Ecology*, **43**, 381-399.

Key, R. (2000) Bare ground and the conservation of invertebrates. *British Wildlife*, **11**, 183-191.

Kiehl, K. & Wagner, C. (2006) Effect of Hay Transfer on Long-Term Establishment of Vegetation and Grasshoppers on Former Arable Fields. *Restoration Ecology*, **14**, 157-166.

Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science*, **23**, 805-821.

Klimkowska, A., Van Diggelen, R., Bakker, J.P. & Grootjans, A.P. (2007) Wet meadow restoration in Western Europe: a quantitative assessment of the effectiveness of several techniques. *Biological Conservation*, **140**, 318-328.

Koivula, M., Punttila, P., Haila, Y. & Niemelä, J. (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, **22**, 424-435.

Kondolf, G.M. & Micheli, E. (1995) Evaluating stream restoration projects. *Environmental Management*, **19**, 1-15.

Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J. & Huss-Danell, K. (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia*, **125**, 271-282.

Kotze, D.J. & O'Hara, R.B. (2003) Species decline - but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, **135**, 138-148.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999) The second silent spring? *Nature*, **400**, 611-612.

Krooss, S. & Schaefer, M. (1998) The effect of different farming systems on epigeic arthropods: a five-year study on the rove beetle fauna (Coleoptera: Staphylinidae) of winter wheat. *Agriculture, Ecosystems & Environment*, **69**, 121-133.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299-305.

Laliberté, E. & Shipley, B. (2011) *FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.*

Lambeets, K., Vandegehuchte, M.L., Maelfait, J.P. & Bonte, D. (2008) Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*, **77**, 1162-1174.

Lambeets, K., Vandegehuchte, M.L., Maelfait, J.P. & Bonte, D. (2009) Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning. *Biological Conservation*, **142**, 625-637.

Lang, A. (2000) The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in Arable Land. *Anzeiger für Schädlingskunde*, **73**, 99-106.

Larwood, G.P. & Funnell, B.M. (1961) The geology of Norfolk. *Transaction of the Norfolk and Norwich Naturalists' Society*, **19**, 270–375.

Lassau, S.A., Hochuli, D.F., Cassis, G. & Reid, C.A.M. (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions*, **11**, 73-82.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, 177-192.

Lawton, J.H., Bignell, D., Bolton, B., Bloemers, G., Eggleton, P., Hammond, P., Hodda, M., Holt, R., Larsen, T. & Mawdsley, N. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, **391**, 72-76.

Leech, A.R. (2000) A breif history of the Holt Lowes. *Holt Lowes Wildlife Group Report No.1 June 2000* (ed. by O. Barnes, J. Clifton, B. Dawson, K. Eradus, S. Harrap, A.R. Leech, A. Starline and D. White), pp. 1-3. Holt Lowes Wildlife Group, Holt, Norfolk.

Legendre, P. & Fortin, M.J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107-138.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam.

Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271-280.

Legendre, P. & Fortin, M.J. (2010) Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources*, **10**, 831-844.

Lepš, J. & Šmilauer, P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge.

Lester, D. & Morrill, W.L. (1989) Activity density of ground beetles (Coleoptera: Carabidae) in alfalfa and sainfoin. *Journal of Agricultural Entomology*, **6**, 71-76.

Liira, J., Issak, M., Jõgar, Ü., Mändoja, M. & Zobel, M. (2009) Restoration management of a floodplain meadow and its cost-effectiveness-the results of a 6-year experiment. *Annales Botanici Fennici.* pp. 397-408. BioOne.

Lindroth, C. (1974) *Coleoptera: Carabidae*. Royal Entomological Society of London, London.

Liu, Y., Axmacher, J., Li, L., Wang, C. & Yu, Z. (2007) Ground beetle (Coleoptera: Carabidae) inventories: a comparison of light and pitfall trapping. *Bulletin of Entomological Research*, **97**, 577-584.

Liu, Y., Axmacher, J.A.N.C., Wang, C., Li, L. & Yu, Z. (2010) Ground beetles (Coleoptera: Carabidae) in the intensively cultivated agricultural landscape of Northern China–implications for biodiversity conservation. *Insect Conservation and Diversity*, **3**, 34-43.

Liu, Y., Axmacher, J.C., Wang, C., Li, L. & Yu, Z. (2011) Ground beetle (Coleoptera: Carabidae) assemblages of restored semi-natural habitats and intensively cultivated fields in Northern China. *Restoration Ecology*, **20**, 234–239.

Loreau, M. (1986) Niche differentiation and community organization in forest carabid communities. *Carabid Beetles, Their Adaptations and Dynamics: Proceedings, 17th International Congress of Entomology, Hamburg* (ed. by P.J. Den Boer, M.L. Luff, D. Mossakowski and F. Weber), pp. 465-487. Gustav Fischer, New York.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804-808.

Lorenz, W. (2005) *Systematic List of Extant Ground Beetles of the World (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae. Rhysodinae).* . Published by the author, Tutzing, Germany.

Lott, D. & Anderson, R. (2011) *The Staphylinidae (Rove Beetles) of Britain and Ireland. Parts 7 & 8: Oxyporinae, Steninae, Euaesthetinae, Pseudopsinae, Paederinae, Staphylininae*. Royal Entomological Society, St Albans.

Lott, D.A. (2001) Ground beetles and rove beetles associated with temporary ponds in England. *Freshwater Forum*, **17**, 40-53.

Lott, D.A. (2003) *An Annotated List of Wetland Ground Beetles (Carabidae) and Rove Beetles (Staphylinidae) Found in the British Isles Including a Literature Review of Their Ecology*. English Nature, Peterborough.

Lott, D.A. (2009) *The Staphylinidae (Rove Beetles) of Britain and Ireland. Part 5: Scaphidiinae, Piestinae, Oxytelinae*. Royal Entomological Society, St Albans.

Lott, D.A. (2011) *The Rove Beetles (Staphylinidae) of Leicestershire and Rutland: Part 1: Sub-families Paederinae, Pseudopsinae and Staphylininae*. Leicestershire Entomological Society, Leicestershire.

Loubère, M. (2010) *Northeastern France Woodlands Coleoptera Ecological Atlas*. Available at: http://www.sibnef1.eu (accessed 13 September 2012).

Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41**, 231-256.

Lövei, G.L., Magura, T., Tóthmérész, B. & Ködöböcz, V. (2006) The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global Ecology and Biogeography*, **15**, 283-289.

Luff, M.L. (1966) The abundance and diversity of the beetle fauna of grass tussocks. *The Journal of Animal Ecology*, 189-208.

Luff, M.L. (1968) Some effects of formalin on the numbers of Coleoptera caught in pitfall traps. *Entomologist's Monthly Magazine*, **104**, 115-116.

Luff, M.L. (1978) Diel activity patterns in some field Carabidae. *Ecological Entomology*, **3**, 53-62.

Luff, M.L. (1996) Use of Carabids as environmental indicators in grasslands and cereals. *Annales Zoologici Fennici*, **33**, 185-195.

Luff, M.L. (1998) *Provisional Atlas of the Ground Beetles (Coleoptera, Carabidae) of Britain*. Institute of Terrestrial Ecology, Huntingdon, UK.

Luff, M.L. (2006) Carabidae. *A Coleopterist's Handbook* (ed. by J. Cooter and M.V.L. Barcley). The Amateur Entomologists' Society, Kent, England.

Luff, M.L. (2007) *The Carabidae (Ground Beetles) of Britain and Ireland*, 2nd edn. Royal Entomological Soctiety, St Albans.

Luff, M.L., Eyre, M.D. & Rushton, S.P. (1989) Classification and ordination of habitats of ground beetles (Coleoptera, Carabidae) in north-east England. *Journal of Biogeography*, **16**, 121-130.

Luo, T.-H., Yu, X.-D. & Zhou, H.-Z. (2013) Effects of reforestation practices on staphylinid beetles (Coleoptera: Staphylinidae) in Southwestern China forests. *Environmental Entomology*, **42**, 7-16.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, New Jersey.

Maddock, A. (2008) *UK Biodiversity Action Plan: Priority Habitat Descriptions* Joint Nature Conservation Committee, Peterborough.

Magura, T. (2002) Carabids and forest edge: spatial pattern and edge effect. *Forest Ecology and Management*, **157**, 23-37.

Magura, T., Tóthmérész, B. & Bordán, Z. (2000) Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. *Biological Conservation*, **93**, 95-102.

Magura, T., Ködöböcz, V. & Tóthmérész, B. (2001a) Effects of habitat fragmentation on carabids in forest patches. *Journal of Biogeography*, **28**, 129-138.

Magura, T., Tóthmérész, B. & Molnár, T. (2001b) Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity & Conservation*, **10**, 287-300.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Wiley-Blackwell, Oxford.

Magurran, A.E. & Henderson, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature*, **422**, 714-716.

Magurran, A.E. & McGill, B.J. (2011a) Challenges and opportunities in the measurement and assessment of biological diversity. *Biological Diversity: Frontiers in Measurement and Assessment* (ed. by A.E. Magurran and B.J. Mcgill), pp. 1-7. Oxford University Press, Oxford.

Magurran, A.E. & McGill, B.J.(eds.) (2011b) *Biological Diversity: Frontiers in Measurement and Assessment.* Oxford University Press, Oxford.

Mainstone, C.P. (1999) *Chalk Rivers, Nature Conservation and Management.* English Nature & Environment Agency, Peterborough.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243-253.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, **94**, 199-209.

Mason, C. & Macdonald, S. (1990) The riparian woody plant community of regulated rivers in eastern England. *Regulated Rivers: Research & Management*, **5**, 159-166.

Mason, C.F. & MacDonald, S.M. (2004) Growth in otter (Lutra lutra) populations in the UK as shown by long-term monitoring. *Ambio*, **33**, 148-152.

Mason, N.W., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112-118.

Maunder, M. (1992) Plant reintroduction: an overview. *Biodiversity & Conservation*, **1**, 51-61.

May, R.M. (1988) How many species are there on earth? *Science*, **241**, 1441.

May, R.M., Lawton, J.H. & Stork., N.E. (1995) Assessing extinction rates. *Extinction Rates* (ed. by R.M. May), pp. 1-24. Oxford University Press, Oxford.

McBride, A., Diack, I., Droy, N., Hamill, B., Jones, P., Schutten, J., Skinner, A. & Street, M. (2011) *The Fen Management Handbook*. Scottish Natural Heritage, Perth.

McCann, K.S. (2000) The diversity–stability debate. *Nature*, **405**, 228-233.

McCracken, D.I. (1994) A fuzzy classification of moorland ground beetle (Coleoptera: Carabidae) and plant communities. *Pedobiologia*, **38**, 12-27.

McCune, B., Grace, J.B. & Urban, D.L. (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.

McDonald, A.W. (2001) Succession during the re-creation of a flood-meadow 1985-1999. *Applied Vegetation Science*, **4**, 167-176.

McGeogh, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, **73**, 181-201.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178-185.

McInnis, M.L. & McIver, J. (2001) Influence of off-stream supplements on stream banks of riparian pastures. *Journal of Range Management*, **54**, 648-652.

McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, 495-516.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450-453.

McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S. & Stuart, S.N. (2007) Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS biology*, **5**, e272.

Michels Jr, G., Carney, V., Jones, E. & Pollock, D. (2010) Species diversity and qualitative assessment of ground beetles (Coleoptera: Carabidae) in three riparian habitats. *Environmental Entomology*, **39**, 738-752.

Middleton, B.A., Holsten, B. & van Diggelen, R. (2006) Biodiversity management of fens and fen meadows by grazing, cutting and burning. *Applied Vegetation Science*, **9**, 307-316.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis*. Island Press, Washington DC.

Miller, J.D. & Gaskin, G.J. (1996) *The Development and Application of the Theta Probe Soil Water Sensor, MLURI Technical Note*. Macaulay Land Use Research Institute, Aberdeen.

Ministry of Defence (2006) *United Kingdom Training Areas: Stanford Map*. MoD, Middlesex.

Mitsch, W.J. & Gosselink, J.G. (1993) *Wetlands*. Van Nostrand Reinhold, New York.

Moore, J.C., Walter, D.E. & Hunt, H.W. (1988) Arthropod regulation of micro-and mesobiota in below-ground detrital food webs. *Annual Review of Entomology*, **33**, 419-435.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G. & Worm, B. (2011) How many species are there on Earth and in the ocean? *PLoS Biology*, **9**, e1001127.

Morris, M.G. (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation*, **95**, 129-142.

Moss, B. (2001) *The Broads: the People's Wetlands*. Harper Collins, London.

Mouchet, M.A., Villeger, S., Mason, N.W. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867-876.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, **10**, 58-62.

Murdoch, W.W., Evans, F.C. & Peterson, C.H. (1972) Diversity and pattern in plants and insects. *Ecology*, 819-829.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858.

Naeem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, **6**, 567-579.

Naiman, R.J. & Decamps, H.(eds.) (1990) *The Ecology and Management of Aquatic-Terrestrial Ecotones*. UNESCO, Paris.

Naiman, R.J. & Décamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621-658.

Naiman, R.J., Decamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*, **3**, 209-212.

Naiman, R.J., Decamps, H. & McClain, M.E. (2005) *Riparia: Ecology, Conservation, and Management of Streamside Communities*. Elsevier, London.

Natural England (2001) *SSSI information for Hooks Well Meadows*. Natural England, Norfolk.

Natural England (2013) *Higher Level Stewardship - Environmental Stewardship Handbook*. Available at: http://publications.naturalengland.org.uk/publication/2827091?category=45001 (accessed 5 November 2013).

New, T.R. (2010) *Beetles in Conservation*. Wiley-Blackwell, Oxford.

Newbold, C., Honnor, J. & Buckley, K. (1989) *Nature Conservation and Management of Drainage Channels*. Nature Conservancy Council, Peterborough.

Newton, I. (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis*, **146**, 579-600.

Nield, C.E. (1976) Aspects of the biology of *Staphylinus olens* (Müller), Britain's largest Staphylinid beetle. *Ecological Entomology*, **1**, 117-126.

Niemalä, J., Halme, E. & Haila, Y. (1990) Balancing sampling effort in pitfall trapping of carabid beetles. *Entomologica Fennica*, **1**, 233-238.

Niemela, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *European Journal of Entomology*, **98**, 127-132.

Niemela, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. (1992) Small-scale heterogeneity in the spatial distribution of carabid beetles in the Southern Finnish taiga. *Journal of Biogeography*, **19**, 173-181.

Niemela, J., Kotze, D.J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D. & de Oca, E.M. (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology*, **17**, 387-401.

Niemelä, J. (1996) From systematics to conservation–carabidologists do it all. *Annales Zoologici Fennici*, **33**, 1-4.

Niemelä, J. & Baur, B. (1998) Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. *Biodiversity & Conservation*, **7**, 1407-1416.

Niemelä, J., Langor, D. & Spence, J.R. (1993) Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conservation Biology*, **7**, 551-561.

Niemelä, J., Haila, Y. & Punttila, P. (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography*, **19**, 352-368.

Nilsson, C. & Svedmark, M. (2002) Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management*, **30**, 468-480.

Nilsson, C., Brown, R.L., Jansson, R. & Merritt, D.M. (2010) The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews*, **85**, 837-858.

Norfolk Biodiversity Partnership (2004) *Norfolk Biodiversity Action Plan: Wet Woodlands*. Available at: http://www.norfolkbiodiversity.org/pdf/SAPsHAPs/HAPs/Wet_woodlands.pdf (accessed 2 November 2013).

North Norfolk District Council (2009) *Landscape Character Assessment of North Norfolk (Draft)*. North Norfolk District Council, Cromer.

Noss, R. (1990) Indicators for monitoring biodiversity: a hierachical approach. *Conservation Biology*, **4**, 355-364.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H. & Graham, R.L. (1988) Indices of landscape pattern. *Landscape Ecology*, **1**, 153-162.

Ødegaard, F. (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, **71**, 583-587.

Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity & Conservation*, **5**, 75-100.

Oksanen, J. (2011) *Multivariate analysis of ecological communities in R: vegan tutorial. R package version 2.0-1*. Available at: http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf (accessed 3 March 2013).

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2012) *vegan: Community Ecology Package*. Available at: http://CRAN.R-project.org/package=vegan (accessed 3 March 2013).

Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027-2039.

Oliver, I., Beattie, A.J. & York, A. (1998) Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. *Conservation Biology*, **12**, 822-835.

Osborne, L., Bayley, P., Higler, L., Statzner, B., Triska, F. & Iversen, T. (1993) Restoration of lowland streams: an introduction. *Freshwater Biology*, **29**, 187-194.

Paetzold, A., Schubert, C. & Tockner, K. (2005) Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. *Ecosystems*, **8**, 748-759.

Paetzold, A., Yoshimura, C. & Tockner, K. (2008) Riparian arthropod responses to flow regulation and river channelization. *Journal of Applied Ecology*, **45**, 894-903.

Pearce, J.L. & Venier, L.A. (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecological Indicators*, **6**, 780-793.

Pearson, D.L. & Cassola, F. (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology*, **6**, 376-391.

Peres-Neto, P.R. & Jackson, D.A. (2001) How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, **129**, 169-178.

Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614-2625.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741-758.

Petchey, O.L. & Gaston, K.J. (2007) Dendrograms and measuring functional diversity. *Oikos*, **116**, 1422-1426.

Peterken, G. & Hughes, F. (1995) Restoration of floodplain forests in Britain. *Forestry*, **68**, 187-202.

Peterken, G.F. & Hughes, F.M.R. (1998) Limitations and opportunities for restoring floodplain forest in Britain. *United Kingdom Floodplains* (ed. by R.G. Bailey, P.V. José and B.R. Sherwood), pp. 423-436. Westbury, Yorkshire.

Petts, G.E. (1990a) Forested river corridors: a lost resource. *Water, Engineering and Landscape* (ed. by D. Cosgrove and G.E. Petts), pp. 12-34. Belhaven Press, London.

Petts, G.E. (1990b) The role of ecotones in aquatic landscape management. *The Ecology and Management of Aquatic-Terrestrial Ecotones* (ed. by R.J. Naiman and H. Decamps), pp. 227-261. UNESCO, Paris.

Petts, G.E. (1998) Floodplain rivers and their restoration: a European perspective. *United Kingdom Floodplains* (ed. by R.G. Bailey, P.V. José and B.R. Sherwood), pp. 29-41. Westbury, Yorkshire.

Petts, G.E. & Bickerton, M.A. (1994) *River Wissey Investigations: Linking Hydrology and Ecology*. Report to the Environment Agency Anglian Region, Birmingham.

Pfiffner, L. & Luka, H. (2000) Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment*, **78**, 215-222.

Pimentel, D., Wilson, C., McCullum, C., Huang, R., Dwen, P., Flack, J., Tran, Q., Saltman, T. & Cliff, B. (1997) Economic and environmental benefits of biodiversity. *BioScience*, **47**, 747-757.

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347.

Pinter, N. (2005) One Step Forward, Two Steps Back on U.S. Floodplains. *Science*, **308**, 207-208.

Podani, J. (1999) Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, 331-340.

Poff, N.L.R., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P. & Kondratieff, B.C. (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, **25**, 730-755.

Prendergast, J., Quinn, R., Lawton, J., Eversham, B. & Gibbons, D. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335 - 337.

Purseglove, J. (1988) *Taming the Flood: A History and Natural History of Rivers and Wetlands*. Oxford University Press, Oxford.

Purtauf, T., Dauber, J. & Wolters, V. (2005) The response of carabids to landscape simplification differs between trophic groups. *Oecologia*, **142**, 458-464.

Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, **405**, 212-219.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Rackham, O. (1994) *The Illustrated History of the Countryside*. Orion Publishing Group, London.

Rainio, J. & Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity & Conservation*, **12**, 487-506.

Resh, V.H., Hildrew, A.G., Statzner, B. & Townsend, C.R. (1994) Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biology*, **31**, 539-554.

Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, **82**, 1112-1129.

Ribera, I., Foster, G.N., Downie, I.S., McCracken, D.I. & Abernethy, V.J. (1999) A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). *Annales Zoologici Fennici*, **36**, 21-37.

Riecken, U. & Raths, U. (1996) Use of radio telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. *Annales Zoologici Fennici.* pp. 109-116. Helsinki: Suomen Biologian Seura Vanamo, 1964-.

Ries, L., Fletcher Jr, R.J., Battin, J. & Sisk, T.D. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, 491-522.

River Glaven Conservation Group (2007) *A Cinderella River: The River Glaven Conservation Group (RGCG) In-River Habitat Improvement 2006*. River Glaven Conservation Group, Norfolk.

River Glaven Conservation Group (2013) *River Glaven Conservation Group website*. Available at: http://www.riverglaven.co.uk/ (accessed 10 September 2013).

Robinson, C.T., Tockner, K. & Ward, J.V. (2002) The fauna of dynamic riverine landscapes. *Freshwater Biology*, **47**, 661-677.

Rodrigues, A.S. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 713-737.

Rodwell, J.S.◊(ed.) (1991) *British Plant Communities*. Cambridge University Press, Cambridge.

Rodwell, J.S. (1992) *British Plant Communities Volume 3. Grasslands and Montane Communities*. Cambridge University Press, Cambridge.

Roni, P.◊(ed.) (2005) *Monitoring Stream and Watershed Restoration*. American Fisheries Society, Bethesda, Mayland.

Rood, S.B. & Mahoney, J.M. (1990) Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management*, **14**, 451-464.

Rose, F., O'Reilly, C., Smith, D. & Collings, M. (2006) *The Wild Flower Key: How to Identify Wild Flowers, Trees and Shrubs in Britain and Ireland*. Frederick Warne, London.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Ruiz-Jaen, M.C. & Mitchell Aide, T. (2005) Restoration success: how is it being measured? *Restoration Ecology*, **13**, 569-577.

Rushton, S., Luff, M. & Eyre, M. (1991) Habitat characteristics of grassland *Pterostichus* species (Coleoptera, Carabidae). *Ecological Entomology*, **16**, 91-104.

Rykken, J.J., Jepson, P.C. & Moldenke, A.R. (2011) Ground-dwelling arthropod distribution and movement across a fragmented riparian forest. *Northwest Science*, **85**, 527-541.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C. & Watts, J. (2005) Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, **86**, 56-62.

Sadler, J.P., Bell, D. & Fowles, A. (2004) The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. *Biological Conservation*, **118**, 41-56.

Sætersdal, M., Gjerde, I., Blom, H.H., Ihlen, P.G., Myrseth, E.W., Pommeresche, R., Skartveit, J., Solhøy, T. & Aas, O. (2003) Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. *Biological Conservation*, **115**, 21-31.

Sala, O.E., Chapin III, S.F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M.n., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.

Sanderson, R., Rushton, S., Cherrill, A. & Byrne, J. (1995) Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. *Journal of Applied Ecology*, **32**, 506-518.

Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.-M., Bieringer, G., Milasowszky, N., Moser, D., Plutzar, C., Pollheimer, M. & Storch, C. (2004) Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biological Conservation*, **117**, 181-190.

Sawada, K. (1972) Methodological researsh in the taxonomy of Aleocharinae. *Contributions from the Biological Laboratory, Kyoto University*, **24**, 31-59.

Schaffers, A.P., Raemakers, I.P., Sýkora, K.V. & ter Braak, C.J.F. (2008) Arthropod assemblages are best predicted by plant species composition. *Ecology*, **89**, 782-794.

Schiegg, K. (2000) Are there saproxylic beetle species characteristic of high dead wood connectivity? *Ecography*, **23**, 579-587.

Schuldt, A. & Assmann, T. (2010) Invertebrate diversity and national responsibility for species conservation across Europe – a multi-taxon approach. *Biological Conservation*, **143**, 2747-2756.

Schuldt, A., Wang, Z., Zhou, H. & Assmann, T. (2009) Integrating highly diverse invertebrates into broad-scale analyses of cross-taxon congruence across the Palaearctic. *Ecography*, **32**, 1019-1030.

Schweiger, O., Maelfait, J.P., Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S. & Bailey, D. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology*, **42**, 1129-1139.

Scott, W.A. & Anderson, R. (2003) Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. *Biological Conservation*, **110**, 197-210.

Seddon, E.L., Wood, P.J., Mainstone, C.P., Greenwood, M.T. & Howard, L.C. (2012) The use of palaeoecological techniques to identify reference conditions for river conservation management. *River Conservation and Management* (ed. by P.J. Boon and P.J. Raven), pp. 211-221. John Wiley & Sons, Chichester.

Sepkoski, J.J., Jr. (1988) Alpha, beta, or gamma: where does all the diversity go? *Paleobiology*, **14**, 221-234.

Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**, 2057-2070.

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, **152**, 738-750.

Siitonen, J. (1994) Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Annales Zoologici Fennici*, **31**, 89-89.

Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, **83**, 247-257.

Similä, M., Kouki, J. & Martikainen, P. (2003) Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management*, **174**, 365-381.

Smith, A.G. (1970) The influence of Mesolithic and Neolithic man on British vegetation. *Studies in the Vegetational History of the British Isles* (ed. by D. Walker and R.G. West), pp. 81-96. Cambridge University Press, Cambridge.

Smith, E.P. & van Belle, G. (1984) Nonparametric estimation of species richness. *Biometrics*, **40**, 119-129.

Smith, P.A., Dosser, J., Tero, C. & Kite, N. (2003) A method to identify chalk rivers and assess their nature conservation value. *Water and Environment Journal*, **17**, 140-144.

Snyder, W.E. & Evans, E.W. (2006) Ecological effects of invasive arthropod generalist predators. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 95-122.

Sobek, S., Steffan-Dewenter, I., Scherber, C. & Tscharntke, T. (2009) Spatiotemporal changes of beetle communities across a tree diversity gradient. *Diversity and Distributions*, **15**, 660-670.

Sober, E. (1986) Philosophical problems for environmentalism. *The Preservation of Species* (ed. by B. Norton), pp. 173-194. Princeton University Press, Princeton, NJ.

Southern, A. (2008) *Implementing an Integrated Approach to Natural Resource Governance: A Case Study in Whole Landscape Design at the Catchment Scale*. PhD Thesis, University of East Anglia.

Southwood, T. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337-365.

Southwood, T. (1988) Tactics, strategies and templets. *Oikos*, 3-18.

Southwood, T., Brown, V. & Reader, P. (1979) The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society*, **12**, 327-348.

Speight, M. (1989) *Saproxylic Invertebrates and Their Conservation*. Council of Europe, Strasbourg.

Spence, J.R. & Niemelä, J.K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist*, **126**, 881-894.

Sroka, K. & Finch, O.-D. (2006) Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation*, **10**, 335-350.

Stan, M. (2011) Contributions to the knowledge on staphylinids (Coleoptera: Staphylinidae) in some riparian ecosystems of south-eastern Romania. *Travaux du Muséum National d'Histoire Naturelle*, **54**, 409-423.

Steel, W.O. (1970) The larvae of the genera of the Omaliinae (Coleoptera: Staphylinidae) with particular reference to the British fauna. *Transactions of the Royal Entomological Society of London*, **122**, 1-47.

Sterba, O., Mekotova, J., Krskova, M., Samsonova, P. & Harper, D. (1997) Floodplain forests and river restoration. *Global Ecology and Biogeography Letters*, **6**, 331-337.

Stewart, A.J.A. & New, T.R. (2007) Insect conservation in temperate biomes: issues, progress and prospects. *Insect Conservation Biology. Proceedings of the Royal Entomological Society's 23rd Symposium*, pp. 1-33. CABI, Wallingford.

Stork, N.E. (1993) How many species are there? *Biodiversity & Conservation*, **2**, 215-232.

Straškrabová, J., Prach, K., Wade, P. & Joyce, C. (1998) Five years of restoration of alluvial meadows: a case study from Central Europe. *European Wet Grasslands* (ed. by C. Joyce and P.W. Pm), pp. 295–303. John Wiley & Sons, Chichester.

Stromberg, J.C. (2001) Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. *Journal of Arid Environments*, **49**, 17-34.

Su, J.C., Debinski, D.M., Jakubauskas, M.E. & Kindscher, K. (2004) Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation Biology*, **18**, 167-173.

Szyszko, J., Vermeulen, H. J. W. and den Boer, P. J. (1996) Survival and reproduction in relation to habitat quality and food availability for *Pterostichus oblongopunctatus* F. (Carabidae, Col.). *Arthropod Natural Enemies in Arable Land: II Survival, Reproduction and Enhancement* (ed. by C.J.H. Booij and L.J.M.F. Den Nijs), pp. 25-40. Aarhus University Press, Oxford.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79-92.

The Royal Society (2003) *Measuring Biodiversity for Conservation*. The Royal Society, London.

Thiele, H. (1977) *Carabid Beetles in Their Environments - A Study on Habitat Selection by Adaptations in Physiology and Behaviour*. Springer-Verlag, New York.

Thomas, G., José, P.V. & Hirons, G. (1995) Wet grassland in the millenium. *Enact*, **3**, 4-6.

Thoms, M.C., Ogden, R.W. & Reid, M.A. (1999) Establishing the condition of lowland floodplain rivers: a palaeo-ecological approach. *Freshwater Biology*, **41**, 407-423.

Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, **77**, 350-363.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65-66.

Tockner, K. & Stanford, J.A. (2002) Riverine flood plains: present state and future trends. *Environmental Conservation*, **29**, 308-330.

Tockner, K., Bunn, S.E., Gordon, C., Naiman, R.J., Quinn, G.P. & Standord, J. (2008) Flood plains: critically threatened ecosystems. *Aquatic Ecosystems: Trends and Global Prospects* (ed. by N.V. Polunin), pp. 45-61. Cambridge University Press, Cambridge.

Tockner, K., Schiemer, F., Baumgartner, C., Kum, G., Weigand, E., Zweimüller, I. & Ward, J.V. (1999) The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers: Research & Management*, **15**, 245-258.

Topping, C. & Sunderland, K. (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, 485-491.

Tottenham, C. (1954) *Coleoptera Staphylinidae Section (a) Piestinae to Euaesthetinae*. Royal Entomological Society, London.

Townsend, C.R. & Hildrew, A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, **31**, 265-275.

Trémolières, M., Sánchez-Pérez, J.M., Schnitzler, A. & Schmitt, D. (1998) Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest. *Plant Ecology*, **135**, 59-78.

Tronquet, M. (2006) *Catalogue Iconographique des Coléoptères des Pyrénées-Orientales. Vol. 1: Staphylinidae. Supplément au Tome XV de la Revue de l'Association Roussillonnaise d'Entomologie*. Association Roussillonnaise d'Entomologie, Perpignan.

Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnology and Oceanography*, **39**, 1440-1454.

Tuomisto, H. & Ruokolainen, K. (2008) Analyzing or explaining beta diversity? Reply. *Ecology*, **89**, 3244-3256.

Uetz, G.W., Van Der Laan, K.L., Summers, G.F., Gibson, P.A. & Getz, L.L. (1979) The effects of flooding on floodplain arthropod distribution, abundance and community structure. *American Midland Naturalist*, **101**, 286-299.

UK Biodiversity Group (1998) *Tranche 2 Action Plans - Volume II: Terrestrial and freshwater habitats*. Joint Nature Conservation Committee, Peterborough.

UNEP (1992) *Convention on Biological Diversity: Article 2: Use of Terms*. United Nations, Rio de Janeiro.

Usher, M., Field, J. & Bedford, S. (1993) Biogeography and diversity of ground-dwelling arthropods in farm woodlands. *Biodiversity Letters*, **1**, 54-62.

van Diggelen, R., Middleton, B., Bakker, J., Grootjans, A. & Wassen, M. (2006) Fens and floodplains of the temperate zone: present status, threats, conservation and restoration. *Applied Vegetation Science*, **9**, 157-162.

Van Vuuren, D.P., Sala, O.E. & Pereira, H.M. (2006) The future of vascular plant diversity under four global scenarios. *Ecology and Society*, **11**, 25.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York.

Verhoeven, J.T.A. & Setter, T.L. (2010) Agricultural use of wetlands: opportunities and limitations. *Annals of botany*, **105**, 155-163.

Villéger, S., Mason, N.W. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290-2301.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882-892.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494.

Wallin, H. & Ekbom, B. (1994) Influence of hunger level and prey densities on movement patterns in three species of *Pterostichus* beetles (Coleoptera: Carabidae). *Environmental Entomology*, **23**, 1171-1181.

Ward, J., Tockner, K. & Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research & Management*, **15**, 125-139.

Ward, J.V. & Stanford, J.A. (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research & Management*, **11**, 105–119.

Warrington, S. (2008) *The National Trust East of England Regional Nature Conservation Strategy*. National Trust, Bury St. Edmunds, Suffolk.

Watford Coleoptera Group (2011) *Species and Family Descriptions*. Available at: http://www.thewcg.org.uk/ (accessed 7th August 2011).

Watkins, W., Clarke, E., Wehl, F., MacDonald, A., Cova, C. & DeVos, S. (2008) *Broadland District Landscape Character Assessment*. Broadland District Council, Norwich.

Weaver, J.C. (1995) Indicator species and scale of observation. *Conservation Biology*, **9**, 939-942.

Weibull, A.-C., Östman, Ö. & Granqvist, Å. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity & Conservation*, **12**, 1335-1355.

Weiher, W. (2011) A primer of trait and functional diversity. *Biological Diversity: Frontiers in Measurement and Assessment* (ed. by A.E. Magurran and B.J. Mcgill), pp. 175-193. Oxford University Press, Oxford.

Weithoff, G. (2003) The concepts of 'plant functional types' and 'functional diversity' in lake phytoplankton - a new understanding of phytoplankton ecology? *Freshwater Biology*, **48**, 1669-1675.

Welling, M. (1990) Dispersal of ground beetles (Col., Carabidae) in arable land. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent*, **55**, 483-491.

Wheeler, R.E. (2010) *lmPerm: Permutation tests for linear models The R project for statistical computing* http://www.r-project.org/.

Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, **30**, 279-338.

Whittaker, R.H. (1965) Dominance and diversity in land plant communities - numerical relations of species express importance of competition in community function and evolution. *Science*, **147**, 250-260.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213-251.

Whittaker, R.H. (1975) *Communitites and Ecosystems*. MacMillan, New York.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.

Wiens, J.A. (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics*, **7**, 81-120.

Wiens, J.A. & Milne, B.T. (1989) Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology*, **3**, 87-96.

Williams, P. & Humphries, C. (1996) Comparing character diversity among biotas. *Biodiversity: A Biology of Numbers and Difference* (ed. by K. Gaston), pp. 54-76. Blackwell Science, Oxford.

Wilson, E.O. (1984) *Biophilia*. Harvard University Press, Massachusetts.

Wilson, E.O. (1987) The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology*, **1**, 344-346.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems & Environment*, **75**, 13-30.

With, K.A. & King, A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology*, **13**, 314-326.

Wood, P. & Petts, G.E. (1999) The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, **13**, 387-399.

Woodcock, B.A. (2005) Pitfall trapping in ecological studies. *Insect Sampling in Forest Ecosystems* (ed. by S. Leather), pp. 37-55. Blackwell, Oxford.

Woodcock, B.A. & Pywell, R.F. (2009) Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. *Biodiversity & Conservation*, **19**, 81-95.

Woodcock, B.A. & McDonald, A.W. (2010) What goes wrong? Why the restoration of beetle assemblages lags behind plants during the restoration of a species rich flood-plain meadow. *Fritillary*, **5**, 21-30.

Woodcock, B.A., McDonald, A.W. & Pywell, R.F. (2011) Can long-term floodplain meadow recreation replicate species composition and functional characteristics of target grasslands? *Journal of Applied Ecology*, **48**, 1070-1078.

Woodcock, B.A., Lawson, C.S., Mann, D.J. & McDonald, A.W. (2006) Effects of grazing management on beetle and plant assemblages during the re-creation of a flood-plain meadow. *Agriculture, Ecosystems & Environment*, **116**, 225-234.

Woodcock, B.A., Pywell, R.F., Roy, D.B., Rose, R.J. & Bell, D. (2005a) Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biological Conservation*, **125**, 193-202.

Woodcock, B.A., Mann, D.J., Mirieless, C., McGavin, G.C. & McDonald, A.W. (2005b) Re-creation of a lowland flood-plain meadow: management implications for invertebrate communities. *Journal of Insect Conservation*, **9**, 207-218.

Woodcock, B.A., Edwards, A.R., Lawson, C.S., Westbury, D.B., Brook, A.J., Harris, S.J., Brown, V.K. & Mortimer, S.R. (2008) Contrasting success in the restoration of plant and phytophagous beetle assemblages of species-rich mesotrophic grasslands. *Oecologia*, **154**, 773-783.

Xu, H., Wu, J., Liu, Y., Ding, H., Zhang, M., Wu, Y., Xi, Q. & Wang, L. (2008) Biodiversity congruence and conservation strategies: a national test. *BioScience*, **58**, 632-639.

Yoccoz, N.G., Nichols, J.D. & Boulinier, T. (2001) Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, **16**, 446-453.

Yu, Z., Liu, Y. & Axmacher, J.C. (2006) Field margins as rapidly evolving local diversity hotspots for ground beetles (Coleoptera: Carabidae) in Northern China. *The Coleopterists Bulletin*, **60**, 135-143.

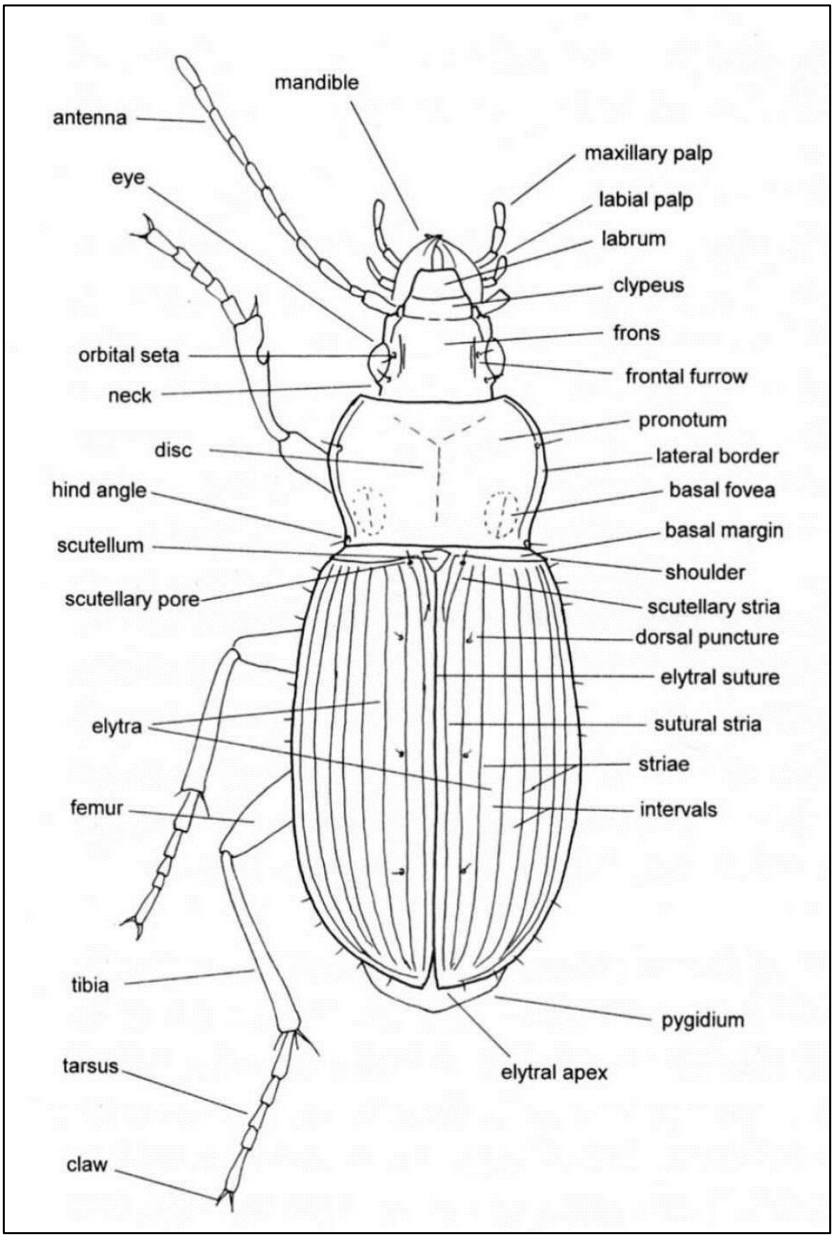
Zedler, J.B. & Kercher, S. (2005) Wetland resources: status, trends, ecosystem services, and restorability. *Annu. Rev. Environ. Resour.*, **30**, 39-74.

Zeigler, D. (2007) *Understanding Biodiversity*. Praeger Publishers, Westport, Connecticut

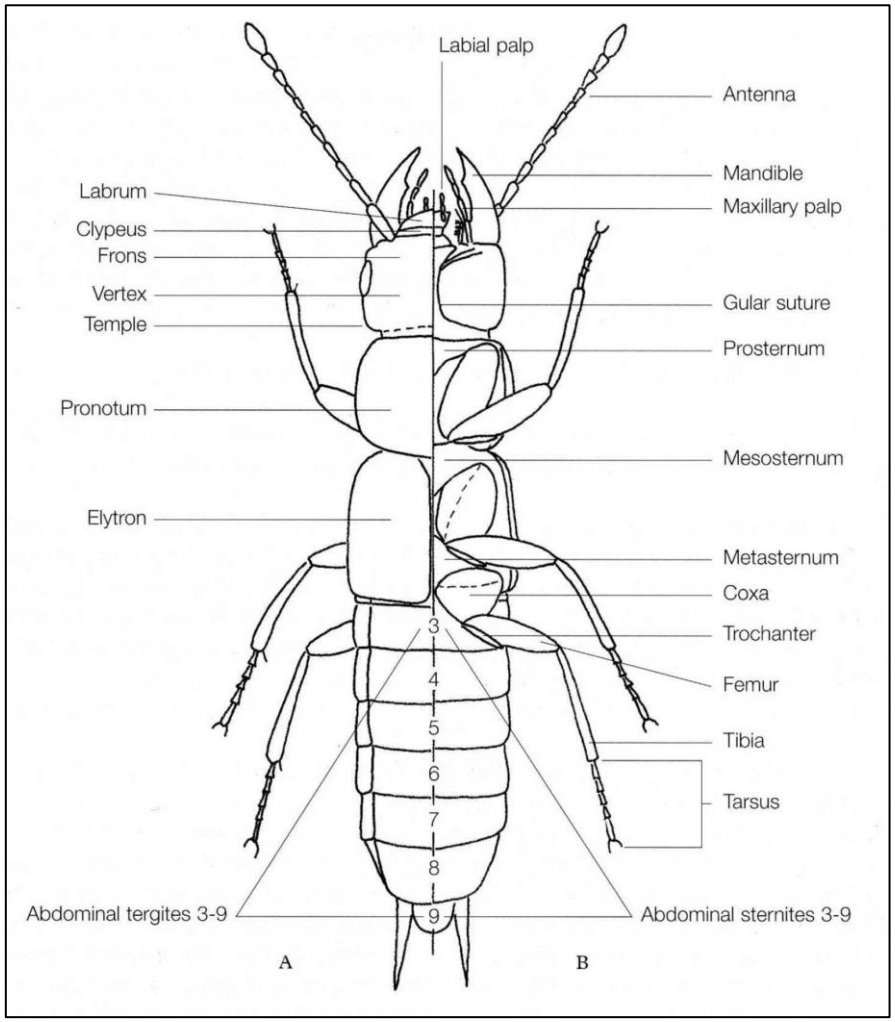
Zulka, K.P. (1994) Carabids in a Central European floodplain: species distribution and survival during inundations. *Carabid Beetles: Ecology and Evolution* (ed. by K. Desender, M. Dufrêne, M. Loreau, M.L. Luff and J.P. Maelfait), pp. 399-405. Springer Netherlands.

Appendix 1

External morphology of an idealised carabid beetle. Diagram from Luff (2007).



External morphology of an idealised staphylinid beetle. Diagram from Lott (2003).



Appendix 2

Site and landscape characteristics for the 15 floodplain sites.

SITE CHARACTERISTICS

Site Code	Site Name	Habitat	Grazing	Cutting	Area (m^2)
HCA	Hunworth Castle	Meadow	Heavy		3766
HM	Hunworth Meadow	Meadow	Heavy		9500
HR	Hunworth Railway	Meadow	Heavy		6105
IB	Ingworth Bridge	Meadow		Cut	8501
MM	Moorgate Meadow	Meadow	Heavy		16304
GF	Glaven Farm	Fen		Cut	3291
HLF	Holt Lowes Fen	Fen	Light		3957
WF	Wildflower Fen	Fen			3502
HLW	Holt Lowes Woodland	Woodland	Light		4209
HW	Hunworth Woods	Woodland			2408
WW	Wildflower Woods	Woodland			4093
MC	Mill Carr	Woodland			8055
RPC	Rough Pasture Carr	Woodland			6964
SC	Shepherd's Carr	Woodland			5643
AC	Alder Carr	Woodland			25876

LANDSCAPE CHARACTRISTICS

Site Code	River	Peri-meter (m)	ED	D_1	Arable	Woodland	Meadow
HCA	Glaven	284	0.075	0.472	5%	15%	70%
HM	Glaven	536	0.056	0.451	60%	20%	10%
HR	Glaven	392	0.064	0.280	45%	10%	40%
IB	Bure	413	0.049	0.194	5%	30%	45%
MM	Bure	752	0.046	0.243	5%	45%	50%
GF	Glaven	223	0.068	0.265	35%	5%	0%
HLF	Glaven	269	0.068	0.096	0%	25%	10%
WF	Glaven	241	0.069	0.155	35%	35%	25%
HLW	Glaven	303	0.072	0.160	5%	30%	10%
HW	Glaven	199	0.083	0.149	20%	50%	15%
WW	Glaven	251	0.061	0.191	30%	40%	10%
MC	Bure	368	0.046	0.069	30%	50%	20%
RPC	Bure	396	0.057	0.032	30%	25%	45%
SC	Bure	296	0.052	0.201	30%	10%	60%
AC	Wissey	889	0.034	0.131	0%	25%	75%

Appendix 3

Estimates of carabid and staphylinid beetle species richness at each sampling site. All standard deviations are analytical. Variances are not calculated for Jacknife 2 and Bootstrap calculations in EstimateS (Colwell, 2009).

CARABIDAE

	Site	Chao 1	Chao 1 SD	Chao 2	Chao 2 SD	Jack 1	Jack 1 SD	Jack 2	Bootstrap
Meadow	HCA	15.2	1.84	16.4	2.82	18.8	1.96	20.6	16.3
	HM	23.0	5.54	29.2	10.7	24.4	1.60	28.8	20.8
	HR	29.0	6.66	34.5	9.46	32.4	2.40	38.4	26.6
	IB	19.3	4.13	20.0	4.52	20.8	1.50	23.5	18.2
	MM	16.0	1.82	16.2	1.85	18.2	2.33	19.3	16.6
Fen	GF	8.0	2.24	8.2	2.14	9.4	1.60	10.8	8.2
	HLF	15.3	4.13	23.2	10.7	18.4	3.25	22.8	14.7
	WF	38.0	16.17	24.8	4.42	27.2	2.94	30.4	23.4
Woodland	HLW	21.0	6.05	18.0	2.61	20.0	1.79	21.7	17.9
	HW	15.0	4.18	13.6	2.15	16.0	3.10	17.2	14.0
	WW	15.5	2.60	26.0	10.96	18.8	0.80	22.4	16.0
	MC	19.5	2.23	19.7	2.11	22.8	3.20	23.7	20.5
	RPC	20.7	1.15	20.5	0.97	23.2	1.50	22.0	21.9
	SC	24.0	6.05	20.3	1.84	23.0	2.19	23.8	21.1
	AC	14.0	1.82	14.3	1.75	16.8	3.75	17.6	14.9

STAPHYLINIDAE

	Site	Chao 1	Chao 1 SD	Chao 2	Chao 2 SD	Jack 1	Jack 1 SD	Jack 2	Bootstrap
Meadow	HCA	20.0	3.42	26.0	7.76	25.0	5.22	29.7	20.2
	HM	31.3	1.62	33.6	3.25	38.0	2.83	40.0	34.0
	HR	23.7	2.21	25.2	3.21	28.4	2.71	30.5	25.1
	IB	34.7	4.49	35.9	4.67	39.6	3.92	43.2	34.6
	MM	22.0	3.42	21.1	2.35	24.6	0.98	25.7	21.9
Fen	GF	21.5	8.18	16.4	2.82	18.8	0.80	20.6	16.3
	HLF	25.5	10.58	19.5	4.38	21.4	2.99	24.4	17.9
	WF	22.0	2.59	23.4	3.57	25.6	0.98	28.0	22.6
Woodland	HLW	45.2	10.86	60.6	20.66	44.4	2.04	53.9	36.1
	HW	26.0	3.42	31.8	7.23	31.8	3.88	36.6	27.0
	WW	25.2	4.34	25.8	4.42	28.2	3.20	31.4	24.4
	MC	25.5	2.90	35.5	9.46	33.4	3.49	39.4	27.6
	RPC	45.0	16.17	31.1	3.83	34.2	2.65	36.9	30.5
	SC	42.3	9.56	37.9	5.27	41.4	3.71	45.6	35.9
	AC	53.3	18.78	46.2	13.29	39.8	4.27	47.6	32.6

Appendix 4

α-diversity indices for carabid and staphylinid beetle assemblages at each sampling sites.

CARABIDAE

	Site	S_{obs}	Specimens	Fisher's α	Shannon Exp.	Simpson's 1/D
Meadow	HCA	14	48	6.64 ± 1.52	9.39	7.57
	HM	18	140	5.49 ± 0.81	7.61	4.55
	HR	22	100	8.72 ± 1.40	13.87	11.41
	IB	16	204	4.07 ± 0.56	8.41	6.53
	MM	15	159	4.06 ± 0.60	8.41	6.54
Fen	GF	7	39	2.49 ± 0.66	4.71	3.84
	HLF	12	63	5.49 ± 0.81	7.61	4.55
	WF	20	185	5.70 ± 0.76	6.75	4.00
Woodland	AC	27	183	3.20 ± 0.47	6.96	5.63
	HLW	16	174	4.29 ± 0.61	8.33	6.48
	HW	12	36	6.30 ± 1.67	9.78	10.5
	MC	18	264	4.37 ± 0.55	7.85	5.46
	RPC	20	629	3.94 ± 0.40	5.87	4.37
	SC	19	589	3.75 ± 0.39	7.24	5.66
	WW	14	316	3.00 ± 0.39	4.81	3.32

STAPHYLINIDAE

	Site	S_{obs}	Specimens	Fisher's α	Shannon Exp.	Simpson's 1/D
Meadow	HCA	17	133	5.18 ± 0.78	4.35	2.24
	HM	30	308	8.22 ± 0.87	8.17	4.16
	HR	22	451	4.18 ± 0.51	4.81	2.91
	IB	30	572	6.74 ± 0.62	5.70	3.24
	MM	19	90	7.36 ± 1.25	9.97	6.14
Fen	GF	14	254	3.19 ± 0.43	2.59	1.62
	HLF	15	146	4.19 ± 0.63	4.44	3.03
	WF	20	418	4.38 ± 0.48	3.97	2.13
Woodland	AC	27	435	6.37 ± 0.64	4.85	3.13
	HLW	30	232	9.18 ± 1.05	11.70	7.66
	HW	23	272	5.99 ± 0.70	6.62	3.55
	MC	23	437	5.17 ± 0.54	5.10	2.98
	RPC	27	274	7.43 ± 0.83	11.25	7.68
	SC	31	508	7.28 ± 0.68	5.53	3.01
	WW	21	401	4.71 ± 0.51	6.69	4.88

Appendix 5

Results of PerMANOVA analysis and *post hoc* pairwise comparisons for carabid and staphylinid beetle site data. Significant values (P_perm) are shown if p<0.05. (NS) Not significant comparisons. Group number corresponds to: GF 1, HM 2, HCA 3, HLF 4, HLW 5, HR 6, HW 7, IB 8, MC 9, MM 10, AC 11, RPC 12, SC 13, WF 14 and WW 15.

CARABIDAE

Source	df	SS	MS	F	P(perm)	P(MC)
SITE	14	135906.5283	9707.6092	4.9579	0.0001	0.0001
Residual	60	117479.7627	1957.9960			
Total	74	253386.2910				

--- Results ---

Pair-wise a posteriori comparisons

Groups	t	P_perm	P_MC
(1, 2)	2.6609	0.0070	0.0018
(1, 3)	2.6077	0.0088	0.0025
(1, 4)	2.2946	0.0079	0.0054
(1, 5)	3.1904	0.0074	0.0001
(1, 6)	1.9334	0.0081	0.0069
(1, 7)	2.7128	0.0083	0.0014
(1, 8)	3.0829	0.0070	0.0005
(1, 9)	2.9507	0.0076	0.0003
(1,10)	2.5139	0.0091	0.0026
(1,11)	4.0144	0.0078	0.0003
(1,12)	3.5496	0.0084	0.0003

Groups	t	P_perm	P_MC
(1,13)	2.5825	0.0080	0.0032
(1,14)	2.9274	0.0087	0.0011
(1,15)	2.1931	0.0074	0.0033
(2, 3)	1.6459	0.0316	0.0362
(2, 4)	1.3146	0.1303	0.1502
(2, 5)	1.7472	0.0078	0.0285
(2, 6)	1.1748	0.1642	0.2412
(2, 7)	2.0695	0.0066	0.0063
(2, 8)	2.1089	0.0066	0.0051
(2, 9)	2.1594	0.0063	0.0077
(2,10)	2.3440	0.0082	0.0044
(2,11)	2.9467	0.0085	0.0011
(2,12)	2.8743	0.0082	0.0009
(2,13)	2.4292	0.0074	0.0037
(2,14)	2.3366	0.0081	0.0030
(2,15)	1.2723	0.0588	0.1787
(3, 4)	1.4707	0.0243	0.0803
(3, 5)	2.1954	0.0083	0.0049
(3, 6)	1.5334	0.0157	0.0517
(3, 7)	1.9499	0.0089	0.0112
(3, 8)	2.4185	0.0085	0.0022
(3, 9)	2.3898	0.0070	0.0023
(3,10)	2.4473	0.0064	0.0024
(3,11)	3.2065	0.0093	0.0007
(3,12)	2.9549	0.0081	0.0008
(3,13)	2.4605	0.0081	0.0029
(3,14)	2.3469	0.0068	0.0027
(3,15)	1.5221	0.0064	0.0492

Groups	t	P_perm	P_MC
(4, 5)	1.5260	0.0523	0.0798
(4, 6)	1.6205	0.0070	0.0354
(4, 7)	2.1945	0.0080	0.0071
(4, 8)	2.5368	0.0091	0.0016
(4, 9)	2.1988	0.0067	0.0049
(4,10)	2.3543	0.0067	0.0026
(4,11)	3.0366	0.0079	0.0016
(4,12)	2.9060	0.0060	0.0009
(4,13)	2.0899	0.0095	0.0076
(4,14)	2.1672	0.0089	0.0070
(4,15)	1.3255	0.0531	0.1345
(5, 6)	2.0346	0.0087	0.0085
(5, 7)	2.3195	0.0079	0.0056
(5, 8)	2.7424	0.0084	0.0013
(5, 9)	2.1447	0.0087	0.0068
(5,10)	2.7795	0.0080	0.0011
(5,11)	2.9290	0.0077	0.0012
(5,12)	2.7597	0.0067	0.0012
(5,13)	2.3505	0.0082	0.0036
(5,14)	1.9669	0.0080	0.0156
(5,15)	1.4267	0.0074	0.0887
(6, 7)	1.7520	0.0074	0.0172
(6, 8)	1.6963	0.0088	0.0215
(6, 9)	2.1819	0.0085	0.0042
(6,10)	1.8780	0.0077	0.0112
(6,11)	2.7972	0.0064	0.0009
(6,12)	2.6031	0.0091	0.0016
(6,13)	1.9901	0.0069	0.0097

Groups	t	P_perm	P_MC
(6,14)	2.1823	0.0079	0.0045
(6,15)	1.3693	0.0337	0.1044
(7, 8)	2.1189	0.0080	0.0038
(7, 9)	2.1197	0.0083	0.0054
(7,10)	2.2816	0.0072	0.0040
(7,11)	2.8671	0.0076	0.0003
(7,12)	2.5231	0.0080	0.0020
(7,13)	2.6192	0.0084	0.0024
(7,14)	1.9792	0.0165	0.0125
(7,15)	1.6815	0.0140	0.0241
(8, 9)	1.7375	0.0244	0.0262
(8,10)	1.9087	0.0076	0.0133
(8,11)	2.6449	0.0081	0.0019
(8,12)	2.4080	0.0078	0.0029
(8,13)	3.1033	0.0082	0.0008
(8,14)	2.5895	0.0069	0.0014
(8,15)	1.6584	0.0065	0.0301
(9,10)	1.5022	0.0140	0.0661
(9,11)	1.5791	0.0671	0.0819
(9,12)	1.4252	0.1013	0.1128
(9,13)	2.6786	0.0070	0.0008
(9,14)	1.8192	0.0154	0.0237
(9,15)	1.2949	0.0858	0.1589
(10,11)	2.8441	0.0080	0.0010
(10,12)	2.5673	0.0074	0.0018
(10,13)	2.5653	0.0071	0.0022
(10,14)	2.5220	0.0072	0.0019
(10,15)	1.7073	0.0096	0.0241

Groups	t	P_perm	P_MC
(11,12)	1.6126	0.0089	0.0651
(11,13)	3.2100	0.0100	0.0006
(11,14)	1.8056	0.0183	0.0332
(11,15)	1.8222	0.0167	0.0239
(12,13)	2.9756	0.0079	0.0005
(12,14)	1.7028	0.0093	0.0416
(12,15)	1.6249	0.0247	0.0446
(13,14)	2.2194	0.0072	0.0054
(13,15)	2.0433	0.0070	0.0083
(14,15)	1.4631	0.0316	0.0868

STAPHYLINIDAE

Source	df	SS	MS	F	P(perm)	P(MC)
SITE	14	95368.4756	6812.0340	5.5044	0.0001	0.0001
Residual	60	74253.6467	1237.5608			
Total	74	169622.1223				

--- Results ---

Pair-wise a posteriori comparisons

Groups	t	P_perm	P_MC
(1, 2)	2.5081	0.0070	0.0034
(1, 3)	2.4866	0.0350	0.0096
(1, 4)	3.6948	0.0079	0.0003
(1, 5)	2.5474	0.0074	0.0019

Groups	t	P_perm	P_MC
(1, 6)	3.8063	0.0081	0.0004
(1, 7)	1.9052	0.0219	0.0258
(1, 8)	3.8466	0.0070	0.0005
(1, 9)	3.3898	0.0076	0.0008
(1,10)	2.8317	0.0091	0.0014
(1,11)	4.7008	0.0078	0.0003
(1,12)	3.0240	0.0084	0.0011
(1,13)	2.9507	0.0080	0.0035
(1,14)	1.5254	NS	0.0928
(1,15)	2.2433	0.0074	0.0066
(2, 3)	1.7708	0.0175	0.0264
(2, 4)	2.5041	0.0089	0.0017
(2, 5)	1.5481	0.0259	0.0552
(2, 6)	1.5120	NS	0.0963
(2, 7)	1.6055	0.0290	0.0514
(2, 8)	1.6739	0.0151	0.0471
(2, 9)	1.5521	0.0317	0.0639
(2,10)	1.7607	0.0082	0.0206
(2,11)	2.1674	0.0085	0.0058
(2,12)	1.8019	0.0082	0.0199
(2,13)	1.3508	NS	0.1545
(2,14)	2.4088	0.0081	0.0023
(2,15)	1.9125	0.0086	0.0142
(3, 4)	2.1896	0.0074	0.0059
(3, 5)	1.8770	0.0083	0.0148
(3, 6)	2.9963	0.0081	0.0013
(3, 7)	1.9027	0.0309	0.0323
(3, 8)	3.1324	0.0085	0.0014

Groups	t	P_perm	P_MC
(3, 9)	2.9111	0.0070	0.0013
(3,10)	1.3936	NS	0.1066
(3,11)	3.5845	0.0093	0.0005
(3,12)	2.3706	0.0081	0.0028
(3,13)	2.3472	0.0248	0.0108
(3,14)	2.8275	0.0068	0.0031
(3,15)	2.4141	0.0064	0.0040
(4, 5)	1.5117	NS	0.0821
(4, 6)	3.5823	0.0070	0.0004
(4, 7)	2.7928	0.0080	0.0025
(4, 8)	3.7149	0.0091	0.0001
(4, 9)	3.3567	0.0067	0.0007
(4,10)	2.1529	0.0067	0.0054
(4,11)	3.9124	0.0079	0.0003
(4,12)	2.7116	0.0060	0.0012
(4,13)	2.6762	0.0095	0.0030
(4,14)	3.6008	0.0089	0.0003
(4,15)	2.9651	0.0083	0.0010
(5, 6)	2.0619	0.0160	0.0166
(5, 7)	1.6949	0.0079	0.0414
(5, 8)	2.4457	0.0084	0.0049
(5, 9)	1.9791	0.0169	0.0163
(5,10)	1.8608	0.0080	0.0162
(5,11)	2.2920	0.0077	0.0048
(5,12)	1.2891	NS	0.1579
(5,13)	1.6398	0.0554	0.0596
(5,14)	2.3730	0.0080	0.0035
(5,15)	1.6574	0.0074	0.0383

Groups	t	P_perm	P_MC
(6, 7)	2.3168	0.0074	0.0084
(6, 8)	1.1500	NS	0.2679
(6, 9)	1.1980	NS	0.2358
(6,10)	2.8234	0.0077	0.0011
(6,11)	2.4224	0.0064	0.0034
(6,12)	2.2533	0.0091	0.0080
(6,13)	1.3081	NS	0.1796
(6,14)	3.0659	0.0079	0.0013
(6,15)	1.9088	0.0183	0.0185
(7, 8)	2.6033	0.0080	0.0027
(7, 9)	1.9664	0.0083	0.0165
(7,10)	2.1340	0.0072	0.0086
(7,11)	3.0475	0.0076	0.0003
(7,12)	1.8043	0.0080	0.0191
(7,13)	1.8650	NS	0.0394
(7,14)	2.1365	0.0093	0.0121
(7,15)	1.4956	NS	0.0934
(8, 9)	1.3297	NS	0.1565
(8,10)	2.9051	0.0076	0.0009
(8,11)	2.4575	0.0081	0.0023
(8,12)	2.7593	0.0078	0.0018
(8,13)	1.3541	NS	0.1398
(8,14)	3.0657	0.0069	0.0019
(8,15)	2.4457	0.0065	0.0036
(9,10)	2.6020	0.0067	0.0017
(9,11)	1.3955	NS	0.1282
(9,12)	2.0144	0.0077	0.0130
(9,13)	0.8154	NS	0.5969

Groups	t	P_perm	P_MC
(9,14)	2.9216	0.0077	0.0014
(9,15)	1.9205	0.0140	0.0228
(10,11)	2.9444	0.0080	0.0006
(10,12)	2.1645	0.0074	0.0037
(10,13)	2.1481	0.0142	0.0112
(10,14)	2.8659	0.0072	0.0013
(10,15)	2.5205	0.0096	0.0018
(11,12)	2.3975	0.0089	0.0038
(11,13)	1.3807	0.0426	0.1405
(11,14)	3.9828	0.0100	0.0003
(11,15)	2.6519	0.0078	0.0029
(12,13)	1.7653	0.0344	0.0352
(12,14)	2.6600	0.0093	0.0019
(12,15)	1.3296	NS	0.1398
(13,14)	2.7115	0.0072	0.0031
(13,15)	1.7649	0.0312	0.0483
(14,15)	2.0222	0.0084	0.0112

Appendix 6

Species lists and abbreviations for carabid and staphylinid beetle and plant species collected over 15 floodplain sites during 2009 and 2010.

CARABIDAE

Species	Abbreviation
Abax parallelepipedus	AbaPar
Acupalpus dubious	AcuDub
Acupalpus parvulus	AcuPar
Agonum emarginatum	AgoEma
Agonum fuliginosum	AgoFul
Agonum micans	AgoMic
Agonum muelleri	AgoMue
Agonum piceum	AgoPic
Agonum thoreyi	AgoTho
Agonum viduum	AgoVid
Amara communis	AmaCom
Amara familiaris	AmaFam
Amara lunicollis	AmaLun
Amara ovata	AmaOva
Anchomenus dorsalis	AncDor
Anisodactylus binotatus	AniBin
Bembidion assimile	BemAss
Bembidion dentellum	BemDen
Bembidion guttula	BemGut
Bembidion lampros	BemLam
Bembidion mannerheimii	BemMan
Bembidion obtusum	BemObt
Bembidion quadrimaculatum	BemQua
Bembidion tetracolum	BemTet
Blemus discus	BleDis
Bradycellus harpalinus	BraHar
Calathus rotundicollis	CalRot
Carabus granulatus	CarGra
Carabus nemoralis	CarNem
Clivina collaris	CliCol
Clivina fossor	CliFos
Cychrus caraboides	CycCar
Elaphrus cupreus	ElaCup
Harpalus rufipes	HarRuf
Leistus fulvibarbis	LeiFul
Loricera pilicornis	LorPil
Nebria brevicollis	NebBre
Notiophilus biguttatus	NotBig
Patrobus atrorufus	PatAtr
Poecilus cupreus	PoeCup
Poecilus versicolor	PoeVer

Species	Abbreviation
Pterostichus diligens	PteDil
Pterostichus madidus	PteMad
Pterostichus melanarius	PteMel
Pterostichus minor	PteMin
Pterostichus niger	PteNig
Pterostichus nigrita agg.	PteNigr
Pterostichus strenuus	PteStr
Pterostichus vernalis	PteVer
Stenolophus mixtus	SteMix
Stenolophus teutonus	SteTeu
Stomis pumicatus	StoPum
Trechus quadristriatus	TreQua

STAPHYLINIDAE

Species	Abbreviation
Anotylus rugosus	AnoRug
Anotylus sculpturatus agg.	AnoScu
Bisnius fimeratus	BisFim
Bolitobius cingulatus	BolCin
Carpelimus corticinus	CarCor
Carpelimus elongatulus	CarElo
Carpelimus erichsoni agg.	CarEri
Coprophilus Striatulus	CopStr
Erichsonius signaticornis	EriSig
Gabrius breviventer	GabBre
Gabrius trossulus	GabTro
Ischnosoma splendidum	IscSpl
Lathrobium brunnipes	LatBru
Lathrobium fovulum	LatFov
Lathrobium fulvipenne	LatFul
Lathrobium geminum	LatGem
Lathrobium longulum	LatLon
Lathrobium terminatum	LatTer
Lesteva heeri	LesHee
Lesteva longoelytrata	LesLon
Lesteva punctata	LesPun
Metopsia clypteata	MetCly
Micropeplus staphylinoides	MicSta
Mycetoporus lepidus	MycLep
Ocypus aeneocephalus	OcyAen
Ocypus brunnipes	OcyBru
Ocypus nitens	OcyNit
Ocypus olens	OcyOle
Olophrum piceum	OloPic
Omalium caesum	OmaCae
Omalium rivulare	OmaRiv
Othius angustus	OthAng

Species	Abbreviation
Othius punctulatus	OthPun
Othius subuliformis	OthSub
Oxytelus fulvipes	OxyFul
Paederus riparius	PaeRip
Philonthus carbonarius	PhiCar
Philonthus cognatus	PhiCog
Philonthus decorus	PhiDec
Philonthus intermedis	PhiInt
Philonthus laminatus	PhiLam
Philonthus marginatus	PhiMar
Philonthus succicola	PhiSuc
Philonthus tenuicornis	PhiTen
Philonthus varians	PhiVar
Proteinus brachypterus	ProBra
Quedius boops	QueBoo
Quedius fuliginosus	QueFul
Quedius fumatus	QueFum
Quedius lateralis	QueLat
Quedius levicollis	QueLev
Quedius maurorufus	QueMau
Quedius molochinus	QueMol
Quedius nemoralis	QueNem
Quedius nicriceps	QueNic
Quedius nitipennis	QueNit
Quedius picipes	QuePic
Quedius schatzmayri	QueSch
Quedius scintillans	QueSci
Quedius semiobscurus	QueSem
Rugilus erichsonii	RugEri
Rugilus orbiculatus	RugOrb
Rugilus rufipes	RugRuf
Sepepophilus marshami	SepMar
Staphylinus erythropterus	StaEry
Stenus aceris	SteAce
Stenus bimaculatus	SteBim
Stenus binotatus	SteBin
Stenus clavicornis	SteCla
Stenus fulvicornis	SteFul
Stenus impressus	SteImp
Stenus juno	SteJun
Stenus lustrator	SteLus
Stenus nitidiusculus	SteNit
Stenus picipes	StePic
Stenus providus	StePro
Stenus pusillus	StePus
Stenus solutus	SteSol
Tachinus humeralis	TacHum
Tachinus marginellus	TacMar
Tachinus rufipes	TacRuf
Tachinus solutus	TacSol

Species	Abbreviation
Tachyporus hypnorum	TacHyp
Tachyporus chrysomelinus	TacCry
Tachyporus dispar	TacDis
Tasigus melanarius	TasMel
Tasigus morsitans	TasMor
Xantholinus linearis	XanLin
Xantholinus longiventris	XanLon

PLANTS

Latin Name	Common name
Acer pseudoplatanus	Sycamore Maple
Adoxa moschatellina	Moschatel
Aesculus hippocastanum	Horse-Chestnet
Agropyron repens	Couch Grass
Agrostis stolonifera	Creeping Bentgrass
Ajuga reptans	Bugle
Alliaria petiolata	Garlic Mustard
Allium ursinum	Ramsons
Alnus glutinosa	Alder
Alopecurus pratensis	Meadow Foxtail
Anemone nemorosa	Wood Anenome
Angelica sylvestris	Wild Angelica
Anthoxanthum odoratum	Sweet Vernal Grass
Arrhenatherum elatius	False Oat-Grass
Arum maculatum	Lords and Ladies
Ballota nigra	Black Horehound
Betula pendula	Silver Birch
Brachypodium sylvaticum	False Brome
Bromus mollis	Soft Brome
Calliergonella cuspidata	Pointed Spear-Moss
Caltha palustris	Marsh Marigold
Cardamine flexuosa	Wavy Bittercress
Cardamine pratensis	Cuckoo Flower
Carex disticha	Brown Sedge
Carex hirta	Hairy Sedge
Carex nigra	Common Sedge
Carex panacea	Carnation Sedge
Carex pendula	Pendulous Sedge
Carex pulicaris	Flea Sedge
Carex remota	Remote Sedge
Carex riparia	Greater Pond Sedge
Cerastium fontanum	Common Mouse-Ear
Chrysosplenium oppositifolium	Opposite-Leaved Golden-Saxifrage
Circaea lutetiana	Enchanter's Nightshade
Cirsium arvense	Creeping Thistle
Cirsium palustre	Marsh Thistle
Conium maculatum	Hemlock
Conopodium majus	Pignut
Corylus avellana	Common Hazel

Latin Name	Common name
Crataegus monogyna	Hawthorn
Cynosurus cristatus	Crested Dog's-Tail
Dactylorhiza fuchsii	Common Spotted Orchid
Dactylorhiza praetermissa	Southern Marsh-Orchid
Dactylis glomerata	Cocksfoot Grass
Dryopteris dilatata	Broad Buckler-Fern
Eleocharis palustris	Common Spike-Rush
Epilobium hirsutum	Great Willowherb
Epilobium montanum	Broad-Leaved Willowherb
Epilobium tetragonum	Square-Stalked Willowherb
Equisetum arvense	Field Horsetail
Equisetum fluviatale	Water Horsetail
Equisetum palustre	Marsh Horsetail
Festuca pratensis	Meadow Fescue
Festuca rubra	Red Fescue
Filipendula ulmaria	Meadowsweet
Fragaria vesca	Woodland Strawberry
Fraxinus excelsior	Common Ash
Galium aparine	Goose Grass
Galium uliginosum	Fen Bedstraw
Geranium robertianum	Herb Robert
Geum urbanum	Wood Avens
Glechoma hederacea	Ground Ivy
Glyceria fluitans	Water Mannagrass
Glyceria maxima	Reed Mannagrass
Hedera helix	Common Ivy
Heracleum sphondylium	Common Hogweed
Holcus lanatus	Yorkshire Fog
Humulus lupulus	Common Hop
Hyacinthoides non-scripta	Common Bluebell
Hydrocotyle vulgaris	Marsh Pennywort
Hypericum tetrapterum	Square-Stemmed St. John's Wort,
Ilex aquifolium	European Holly
Iris pseudacorus	Yellow Iris
Juncus articulatus	Jointed Rush
Juncus conglomeratus	Compact Rush
Juncus effusus	Soft Rush
Juncus inflexus	Hard Rush
Lathyrus pratensis	Meadow Vetchling
Leontodon hispidus	Rough Hawkbit
Listera ovata	European Common Twayblade
Lolium/Festuca rubra	Ryegrass/Fescue Hybrid
Lonicera periclymenum	Honeysuckle
Lotus pedunculatus	Greater Bird's-Foot-Trefoil
Luzula multiflora	Heath Woodrush
Lychnis flos-cuculi	Ragged Robin
Lysimachia nemorum	Yellow Pimpernel
Marchantia spp.	Liverwort
Mentha aquatica	Water Mint
Mercurialis perennis	Dog's Mercury

Latin Name	Common name
Moss	Moss
Moehringia trinervia	Three-Nerved Sandwort
Mycelis muralis	Wall Lettuce
Myosotis laxa	Tufted Forget-Me-Not
Myosotis x suzae	Forget- Forget-Me-Not
Pedicularis palustris	Marsh Lousewort
Phalaris arundinacea	Reed Canary grass
Phragmites australis	Common Reed
Plantago lanceolata	Ribwort Plantain
Poa nemoralis	Wood Bluegrass
Poa pratensis	Smooth Meadow-Grass
Poa trivialis	Rough-Stalked Meadow-Grass
Populus tremula	Aspen
Potentilla erecta	Common Tormentil
Potentilla sterilis	Barren Strawberry
Primula vulgaris	English Primrose
Prunus avium	Wild Cherry
Prunus padus	Bird Cherry
Prunus spinosa	Blackthorn
Pulicaria dysenterica	Fleabane
Quercus robur	Pedunculate Oak
Ranunculus acris	Meadow Buttercup
Ranunculus ficaria	Lesser Celandine
Ranunculus flammula	Lesser Spearwort
Ranunculus repens	Creeping Buttercup
Rhinanthus minor	Yellow Rattle
Ribes rubrum	Redcurrant
Rosa canina	Dog Rose
Rubus fruticosus agg.	Blackberry
Rumex acetosa	Common Sorrel
Rumex crispus	Curled Dock
Rumex obtusifolius	Broad-Leaved Dock
Sambucus nigra	Elder
Scrophularia auriculata	Water Figwort
Senecio jacobaea	Ragwort
Silene dioica	Red Campion
Sisymbrium officinale	Hedge Mustard
Solanum dulcamara	Bittersweet Nightshade
Sorbus aucuparia	Rowan
Stachys sylvatica	Hedge Woundwort
Stellaria alsine	Bog Stitchwort
Stellaria graminea	Lesser Stitchwort
Stellaria Media	Stichwort
Succisa pratensis	Devil's-Bit Scabious
Taraxacum officinale	Dandelion
Trifolium repens	White Clover
Ulmus glabra	Wych Elm
Urtica dioica	Stinging Nettle
Valeriana dioica	Marsh Valerian
Veronica montana	Wood Speedwell

Latin Name	Common name
Veronica officinalis	Heath Speedwell
Veronica serpyllifolia	Thyme-Leaved Speedwell
Viburnum opulus	Guelder Rose
Vicia cracca	Tufted Vetch
Viola odorata	Sweet Violet

Appendix 7

Species lists and abbreviations for carabids, staphylinids and plant species samples at Alder Carr on the River Wissey over the two-week sampling period in April-May 2010.

CARABIDAE

Species	Abbreviation
Agonum emarginatum	AgoEma
Agonum fuliginosum	AgoFul
Amara communis	AmaCom
Anisodactylus binotatus	AniBin
Asphidion Curtum	AspCur
Bembidion biguttatum	BemBig
Bembidion guttula	BemGut
Bembidion mannerheimii	BemMan
Bembidion obtusum	BemObt
Bembidion tetracolum	BemTet
Carabus granulatus	CarGra
Clivina fossor	CliFos
Elaphrus cupreus	ElaCup
Loricera pilicornis	LorPil
Nebria brevicollis	NebBre
Notiophilus biguttatus	NotBig
Patrobus atrorufus	PatAtr
Poecilus versicolor	PoeVer
Pterostichus diligens	PteDil
Pterostichus minor	PteMin
Pterostichus nigrita agg.	PteNigr
Pterostichus strenuus	PteStr

STAPHYLINIDAE

Species	Abbreviation
Anotylus rugosus	AnoRug
Anotylus sculpturatus agg.	AnoScu
Anthobium atrocephalum	AntAtr
Bisnius fimeratus	BisFim
Carpelimus elongatulus	CarElo
Gabrius trossulus	GabTro
Gyrohypnus angustatus	GyrAng
Gyrohypnus fracticornis	GyrFra
Lathrobium brunnipes	LatBru
Lathrobium geminum	LatGem
Lesteva longoelytrata	LatLon
Omalium caesum	OmaCae
Omalium rivulare	OmaRiv
Omalium rugatum	OmaRug

Species	Abbreviation
Othius punctulatus	OthPun
Oxytelus fulvipes	OxyFul
Philonthus carbonarius	PhiCar
Philonthus cognatus	PhiCog
Philonthus decorus	PhiDec
Philonthus intermedis	PhiInt
Philonthus laminatus	PhiLam
Philonthus marginatus	PhiMar
Philonthus micans agg.	PhiMic
Platystethus nitens	PlaNit
Quedius fuliginosus	QueFul
Quedius fumatus	QueFum
Quedius humeralis	QueHum
Quedius maurorufus	QueMau
Quedius schatzmayri	QueSch
Quedius scintillans	QueSci
Stenus bimaculatus	SteBim
Stenus binotatus	SteBin
Stenus juno	SteJun
Stenus nitidiusculus	SteNit
Stenus picipes	StePic
Stenus providus	StePro
Tachinus marginellus	SteLus
Tachinus rufipes	TacMar
Tachyporus dispar	TacRuf
Tasigus melanarius	TasMel
Xantholinus linearis	XanLin
Xantholinus longiventris	XanLon

PLANTS

Latin Name	English Name
Acer pseudoplatanus	Sycamore Maple
Adoxa moschatellina	Moschatel
Agrostis stolonifera	Creeping Bentgrass
Ajuga reptans	Bugle
Alliaria petiolata	Garlic Mustard
Alnus glutinosa	Alder
Anemone nemorosa	Wood Anenome
Angelica sylvestris	Wild Angelica
Anthriscus sylvestris	Cow Parsely
Arctium minus	Burdock
Arum maculatum	Lords and Ladies
Brachypodium sylvaticum	False Brome
Buxus sempervirens	Box
Cardamine flexuosa	Wavy Bittercress
Cardamine pratensis	Cuckoo Flower
Carex remota	Remote Sedge

Latin Name	English Name
Carex riparia	Greater Pond Sedge
Chaerophyllum temulum	Rough Chervil
Cirsium palustre	Marsh Thistle
Conium maculatum	Hemlock
Corylus avellana	Common Hazel
Crataegus monogyna	Hawthorn
Dryopteris dilatata	Broad-Buckler Fern
Eleocharis palustris	Common Spike-Rush
Epilobium montanum	Broad-Leaved Willowherb
Eupatorium cannabinum	Hemp-Agrimony
Fagus sylvatica	Beech
Filipendula ulmaria	Meadowsweet
Fraxinus excelsior	Common Ash
Galeopsis tetrahit	Common Hemp Nettle
Galium aparine	Goose Grass
Galium palustre	Marsh Bedstraw
Geranium robertianum	Herb Robert
Geum urbanum	Wood Avens
Glechoma hederacea	Ground-Ivy
Glyceria fluitans	Water Manna Grass
Hedera helix	Common Ivy
Humulus lupulus	Common Hop
Iris pseudacorus	Yellow Iris
Juncus effusus	Soft Rush
Lamiastrum galeobdolon	Yellow Archangel
Lychnis flos-cuculi	Ragged Robin
Lycopus europeaus	Gypsywort
Lysimachia nummularia	Creeping Jenny
Mentha aquatica	Water Mint
Moehringia trinervia	Three-Nerved Sandwort
Mycelis muralis	Wall Lettuce
Myosotis scorpioides	Water Forget-Me-Not
Paris quadrifolia	Herb Paris
Phalaris arundinacea	Reed Canary Grass
Phragmites australis	Common Reed
Poa pratensis	Smooth Meadow-Grass
Populus canescens	Grey Poplar
Prunus padus	Bird Cherry
Quercus robur	Pedunculate Oak
Ranunculus ficaria	Lesser celandine
Ranunculus repens	Creeping Buttercup
Ribes nigrum	Blackcurrant
Ribes rubrum	Redcurrant
Rubus fruticosus agg.	Blackberry
Salix alba	White Willow
Salix cinerea	Grey Willow
Salix fragilus	Crack Willow
Sambucus nigra	Elder
Sisymbrium officinale	Hedge Mustard
Solanum dulcamara	Bittersweet Nightshade

Latin Name	English Name
Stachys sylvatica	Hedge Woundwort
Stellaria media	Common Chickweed
Tamus communis	Black Bryony
Taraxacum agg.	Dandelion
Ulmus spp.	Elm
Urtica dioica	Stinging Nettle
Valeriana dioica	Marsh Valerian

Appendix 8

Carabid and staphylinid traits. Functional trait information was obtained from a wide range of literature sources (Hinton & Stephens, 1941; Frank, 1968; Kasule, 1968; Nield, 1976; Thiele, 1977; Dennis, 1989; Grafius & Warner, 1989; Buse & Good, 1993; Dennis & Sotherton, 1994; Anderson, 1997; Glesne, 1998; Luff, 1998; Betz, 1999; Ribera et al., 2001; Lott, 2003; Boháč et al., 2007; Clough et al., 2007; Honek et al., 2007; Luff, 2007; Lott, 2009; Sobek et al., 2009; Loubère, 2010; Lott & Anderson, 2011; Watford Coleoptera Group, 2011).

Variables are coded as: Colour- Dark 1, Metallic 2, Pale 3; Pronotum shape- Oval 1, Cordiform 2, Trapezoidal 3; Wing development- Apterous/Brachypterous 1, Dimorphic 2, Macropterous 3; Canopy preference- Open 1, Closed 2, No preference 3; Moisture preference- Dry 1, Wet 2, No preference 3; Breeding season- Spring 1, Summer 2, Autumn/Winter 3; Feeding guild- Predator 1, Herbivore 2, Detritivore 3, Fungivore 4, Omnivore 5; Diel activity: Nocturnal 1, Diurnal 2, Both 3.

CARABIDAE

Species	Size	Colour	Pronotum	Wing Development	Canopy Preference	Moisture Preference	Breeding Season	Feeding Guild	Diel Activity
Abax parallelepipedus	19.5	1	3	1	2	2	1	1	1
Acupalpus dubious	2.7	3	1	3	3	2	1	1	1
Acupalpus parvulus	3.5	3	1	3	3	2	1	1	1
Agonum emarginatum	8.3	1	1	3	3	2	1	1	1
Agonum fuliginosum	6.3	1	1	2	3	2	1	1	3
Agonum micans	6.8	2	1	3	2	2	1	1	3
Agonum muelleri	8.0	2	1	3	1	3	1	1	3
Agonum piceum	6.3	1	1	3	1	2	1	1	1
Agonum thoreyi	7.0	1	1	3	1	2	1	1	1
Agonum viduum	8.3	1	1	3	1	2	1	1	1
Amara communis	7.0	1	3	3	1	3	1	2	2
Amara familiaris	6.4	1	3	3	1	1	1	2	2
Amara lunicollis	8.3	1	3	3	1	1	1	2	2
Amara ovata	8.8	1	3	3	1	1	1	2	3
Anchomenus dorsalis	7.0	2	2	3	1	1	1	1	1
Anisodactylus binotatus	11.5	1	1	3	1	2	1	2	1
Bembidion assimile	3.3	1	2	2	1	2	1	1	1
Bembidion dentellum	5.6	1	2	3	2	2	1	1	2
Bembidion guttula	3.3	1	1	2	3	2	1	1	1
Bembidion lampros	3.5	1	2	2	1	1	1	1	2
Bembidion mannerheimii	3.1	1	1	1	2	2	1	1	1
Bembidion obtusum	3.2	3	1	2	1	1	3	1	1
Bembidion quadrimaculatum	3.1	3	2	2	1	1	1	2	2
Bembidion tetracolum	5.5	3	2	2	1	2	1	1	1
Bradycellus harpalinus	4.4	1	1	3	3	1	3	2	1

Species	Size	Colour	Pronotum	Wing Development	Canopy Preference	Moisture Preference	Breeding Season	Feeding Guild	Diel Activity
Calathus rotundicollis	9.5	1	1	2	2	3	3	1	1
Carabus granulatus	19.5	2	3	2	3	2	1	1	1
Carabus nemoralis	23.0	2	3	1	3	1	1	1	1
Clivina collaris	5.5	3	1	3	3	2	1	1	1
Clivina fossor	6.4	1	1	2	1	3	1	1	1
Cychrus caraboides	16.5	1	1	1	2	3	3	1	1
Elaphrus cupreus	8.8	2	3	3	3	2	1	1	2
Harpalus rufipes	13.5	1	3	3	1	1	3	2	1
Leistus fulvibarbis	7.5	1	2	3	2	2	2	1	1
Loricera pilicornis	7.0	1	2	3	3	2	2	1	1
Nebria brevicollis	12.5	1	2	3	3	3	3	1	1
Notiophilus biguttatus	5.5	2	2	2	3	3	1	1	2
Patrobus atrorufus	8.5	1	2	1	3	3	3	1	1
Poecilus cupreus	12.0	2	1	3	1	1	1	1	3
Poecilus versicolor	11.5	2	1	3	1	2	2	1	2
Pterostichus diligens	6.3	1	1	2	2	2	1	1	1
Pterostichus madidus	12.5	1	1	1	3	3	3	2	1
Pterostichus melanarius	15.0	1	3	2	2	3	3	1	1
Pterostichus minor	7.4	1	3	2	3	2	1	1	1
Pterostichus niger	18.5	1	3	3	3	3	3	1	1
Pterostichus nigrita agg.	10.5	1	3	3	3	2	1	1	1
Pterostichus strenuus	6.6	1	3	2	3	3	1	1	1
Pterostichus vernalis	6.8	1	3	2	2	2	1	1	1
Stenolophus mixtus	5.5	1	1	3	3	2	1	2	1
Stenolophus teutonus	6.0	3	1	2	1	2	1	2	1
Stomis pumicatus	7.5	1	2	1	3	2	1	1	1
Trechus quadristriatus	3.9	1	1	3	1	1	3	1	1

STAPHYLINIDAE

Species	Size (mm)	Feeding	Canopy	Moisture
Anotylus rugosus	4.75	3	3	2
Anotylus sculpturatus agg.	4	3	3	3
Anthobium atrocephalum	2.75	3	2	3
Bisnius fimetarius	6.25	1	1	3
Bolitobius cingulatus	8	1	2	3
Carpelimus corticinus	2.25	5	3	2
Carpelimus elongatulus	2.5	5	3	2
Carpelimus erichsoni agg.	3.5	5	3	2
Coprophilus Striatulus	6.75	2	3	2
Gabrius breviventer	4.25	1	1	2
Gabrius trossulus	4.5	1	3	2
Gyrohypnus angustatus	6.5	1	3	3
Gyrohypnus fracticornis	7	1	3	3

Species	Size (mm)	Feeding	Canopy	Moisture
Ischnosoma splendidum	4	4	3	3
Lathrobium brunnipes	8.75	1	3	2
Lathrobium fovulum	6.5	1	3	2
Lathrobium fulvipenne	8.5	1	1	2
Lathrobium geminum	9	1	1	2
Lathrobium longulum	4.5	1	3	2
Lathrobium terminatum	6.25	1	3	2
Lesteva Heeri	2.95	1	3	2
Lesteva longoelytrata	4.5	1	3	2
Lesteva punctata	3.75	1	3	2
Metopsia clypteata	2.35	4	3	3
Micropeplus staphylinoides	2	4	3	3
Mycetoporus lepidus	4.25	4	3	3
Ocypus aeneocephalus	13	1	3	3
Ocypus brunnipes	14	1	3	3
Ocypus olens	27.5	1	3	3
Olophrum piceum	5.5	3	2	2
Omalium caesum	2.6	3	3	3
Omalium rivulare	3.2	3	1	3
Omalium rugatum	3.5	3	2	3
Othius angustus	5.5	1	3	3
Othius punctulatus	11	1	2	2
Othius subuliformis	5	1	3	3
Oxytelus fulvipes	4.4	3	2	2
Paederus riparius	8	1	3	2
Philonthus carbonaris	7.5	1	3	2
Philonthus cognatus	9.5	1	3	2
Philonthus decorus	12	1	2	2
Philonthus intermedius	10.5	1	3	3
Philonthus laminatus	11	1	3	2
Philonthus marginatus	8.25	1	3	2
Philonthus micans agg.	6.75	1	3	2
Philonthus succicola	11.5	1	3	3
Philonthus tenuicornis	10	1	3	3
Philonthus varians	7	1	3	3
Platystethus nitens	2.75	2	3	2
Proteinus brachypterus	1.75	4	2	3
Quedius boops	5	1	1	3
Quedius fuliginosus agg.	11.5	1	3	2
Quedius fumatus	8.5	1	2	3
Quedius humeralis	7	4	2	3
Quedius lateralis	12	5	3	3
Quedius levicollis	12	1	1	3
Quedius maurorufus	7	1	3	2
Quedius molochinus	10	1	3	2
Quedius nemoralis	6.75	1	3	2
Quedius nicriceps	8.5	1	2	2
Quedius nitipennis	6.25	1	3	2
Quedius picipes	10	1	3	2

Species	Size (mm)	Feeding	Canopy	Moisture
Quedius schatzmayri	6	1	3	2
Quedius scintillans	5.25	1	3	2
Quedius semiobscurus	8.5	1	1	1
Rugilus erichsonii	4.25	1	3	2
Rugilus orbiculatus	4.5	1	3	1
Rugilus rufipes	5.75	1	3	2
Sepepophilus marshami	4.75	4	1	3
Staphylinus erythropterus	16	1	1	3
Stenus aceris	4.5	1	3	3
Stenus bimaculatus	6.75	1	2	2
Stenus binotatus	5.5	1	3	2
Stenus clavicornis	5.75	1	3	3
Stenus fulvicornis	3.5	1	1	2
Stenus impressus	4.5	1	3	3
Stenus juno	6.5	1	3	2
Stenus lustrator	5.25	1	3	2
Stenus nitidiusculus	5	1	3	2
Stenus picipes	4.75	1	1	2
Stenus providus	5.75	1	1	2
Stenus pusillus	2.5	1	1	2
Stenus solutus	5.75	1	3	2
Tachinus humeralis	7	4	2	3
Tachinus marginellus	3.4	1	3	3
Tachinus rufipes	5.5	1	3	3
Tachinus solutus	3.75	5	3	3
Tachyporus dispar	3.4	1	3	3
Tachyporus hypnorum	3.5	1	3	2
Tachyporus chrysomelinus	3.4	1	3	3
Tasigus melanarius	15.5	1	3	3
Tasigus morsitans	14	1	1	1
Xantholinus linearis	7.5	1	1	1
Xantholinus longiventris	7.75	1	1	3